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EFFECTS OF ENVIRONMENTAL CONDITIONS ON CHARACTERISTICS OF
PRESCRIBED FIRES AND RESPROUTING OF HARDWOODS IN SHORTLEAF PINE-
OAK-HICKORY ECOSYSTEMS OF THE UNITED STATES

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Biological Sciences

by
Tracy Lynn Hmielowski
B.S., Florida State University, 2004
August 2013

ACKNOWLEDGMENTS

First, I would like to thank my committee, Dr. Kevin Robertson, Dr. William Platt, Dr. Matthew Slocum, Dr. Philip Stouffer, Dr. Bret Elder, and my dean's representatives, Dr. Jeremy Allison and Dr. Richard Bengtson. Dr. William Platt took me on as a student in 2007, and was willing to co-chair my committee with Dr. Kevin Robertson. As an adviser Kevin provided support, space, equipment, assistance in the field (sometimes in the form of his oldest child!), and patience even when things were not going as planned. Matt offered a great deal of statistical advice throughout this process, as well as helpful discussions about the design of the project. Matt was also an helpful in the analysis and writing of the path analysis chapter. Bill, Phil, and Bret offered insightful advice and comments on the project and written chapters. I would also like to thank Dr. James Geaghan, who offered advice on the ANCOVA analysis of the shadehouse data set.

I am also grateful to everyone who helped me while conducting field work at Tall Timbers Research Station. I was always in search of help with data collection, plot preparation, maintaining the shadehouse project, and conducting prescribed fires. The willingness of George Bruner, David Forsyth, Jason Isbell, Bryan Kreiter, Meredith Leidy, Josh Picott, Kristin Politano, Angie Reid, Eden Robertson, and Parker Titus to assist in these duties is something that I cannot express enough appreciation for. The staff and interns at Tall Timbers throughout the years also deserve many thanks. Eric Staller, the land manager at Tall Timbers, deserves many thanks, as he was willing to let me put over 100 randomly placed plots on the property knowing that we would have to keep equipment and fire out of them for four years.

While at Louisiana State University, I was fortunate to work with a great group of fellow graduate students. Mindy Brooks, Becky Carmichael, Rae Crandall, Darin Ellair, Demetra

Kandelepas, Ellen Leichy, and Yalma Vargas have all shared space, ideas, advice, and office equipment battles with me over the years. Having all of these individuals in the program ahead of me meant that there was always someone who had faced similar challenges and had helpful suggestions on how to handle problems.

In addition to those who have helped me with the hands on aspects of the project, there are those who have acted as my support system, and family of sorts, throughout this process. Metha Klock has been a go-to person due to her willingness to listen when needed, give advice when asked, and give feedback on numerous presentations. In addition to being my coffee buddy on campus, Metha and Erin Herad opened their home to me on countless occasions, and wherever I am they will always be welcome. Becky has also been a great supporter throughout grad school, mainly due to our shared sense of humor. Without Becky and Brett I'm not sure who else I would have had around to enjoy sarcasm, sushi, and homemade beverages. Demetra and Shafe have also been amazing friends while in Louisiana, and I look forward to spending time with them at future ESA meetings. And of course, Bryan Kreiter, who has shared in the challenges and victories of this process. His patience, support, and confidence in me throughout these years have helped me to complete this process.

Last, but not least, I would like to thank my family. My parents and brother who have always been supportive of my graduate program, even if I did have to miss out on more than one holiday with them.

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ABSTRACT

Fire is an essential process for maintaining pine-dominated ecosystems in the southeastern United States. Fire opens space for pine recruitment, consumes fine fuels, stimulates flowering of herbaceous plants, and topkills woody plants. Topkill is the death of the aboveground portion of the plant, which does not necessarily lead to mortality. Most of the woody species in these ecosystems are able to resprout following topkill, sprouting new shoots from meristems at the base of the plant. In the absence of fire, pine-dominated ecosystems transition to closed canopy hardwood forests. Prescribed fires can be applied to mimic the historical fire regime, but the selected time since fire, season of burn, and ignition techniques used can influence both fire characteristics and the response of vegetation. In this dissertation, I explore the effects of prescribed fire treatments on fire characteristics and hardwood resprouting by applying prescribed fires to plots in a shortleaf pine-oak-hickory woodland in north Florida. Fireline intensity, residence times, and heat released per unit area increased progressively with longer time since fire treatment. Reaction intensity, on the other hand, decreased with time since fire, attributable to increased fuel bulk density. Fireline intensity was dampened by greater fuel moisture in the growing season and was greatest with head fire ignitions. I evaluated the response of hardwoods to prescribed fires using a path analysis model. The results of this model suggest that one-year post-fire biomass is mediated via the size and root reserves at the time of topkill, while the characteristics of the fire do not have an effect. I conducted a shadehouse experiment to test for the effects of season and method of topkill on hardwood genets. Genets topkilled in the growing season had reduced resprouting biomass compared to topkill in the dormant season. There was not a difference in biomass between burned and clipped plants. The

results of this study suggest that the response of hardwoods to fire in savanna ecosystems is mediated by the size and resource allocation of plants rather than the intensity of fires.

CHAPTER ONE: INTRODUCTION

One of the most important ecosystem processes shaping and maintaining the structure and function of savanna ecosystems is the death of aboveground woody plant tissues by frequent fires. The two-layered structure of savannas, where canopy trees are widely spaced and the majority of woody stems are limited to the herbaceous layer (Hoffmann et al. 2009, Schutz et al. 2009), is maintained, in part, by frequent fire limiting the size of woody shrubs. Fire often kills aboveground stems and leaves (i.e. topkill), after which resprouting stems are formed from dormant buds at the base of the plant from carbohydrates stored in the roots (Bowen and Pate 1993, El Omari et al. 2003). When fire is excluded and frequent topkill no longer occurs, the landscape becomes dominated by woody species (Means 1996, Scholes and Archer 1997, Waldrop et al. 1992). This shift to woody dominance alters the structure of savanna ecosystems and can decrease the likelihood a site will burn in the future (see Scholes and Archer 1997) changing the overall ecosystem function and species composition.

Management and conservation of savanna ecosystems often involves the use of prescribed fire. The application of prescribed fire can influence fire behavior (Williams et al. 1998, Govender et al. 2006, Robertson and Ostertag 2007) and the response of woody vegetation (Waldrop et al. 1992, Hoffman and Solbrig 2003). Short fire return intervals may provide little time for genets to accumulate carbohydrate storage in the roots, and seasonal changes in carbohydrate allocation between aboveground and belowground structures can limit root reserves available for resprouting (see Robbins and Myers 1992, Werner and Prior 2013). Woody species in savanna ecosystems may maintain greater root reserves belowground (Schutz et al. 2009) and have rapid aboveground growth rates (Hoffman and Solbrig 2003) as adaptations to frequent fire. The pine-dominated ecosystems of the southeastern United States are an example of how

prescribed fire can be used to limit the size and density of woody species and maintain the open structure that characterizes savanna ecosystems.

Pine-dominated ecosystems across the southeastern U.S. Coastal Plain were once almost continuous across the landscape. These pine ecosystems historically occupied the Coastal Plain from Virginia to Florida and west into Louisiana, Texas, and Arkansas. Across this geographic range dominant tree species included *Pinus palustris* (longleaf pine), *P. taeda* (loblolly pine), *P. echinata* (shortleaf pine), and *P. elliottii* (slash pine) (Landers et al. 1995, Haywood et al. 1998, Platt 1999, Hedman et al. 2000). These pine-dominated ecosystems (referred to as pine savannas, pine grasslands, and pine woodlands) have unique aspects of species composition, but similar structural characteristics. Historical accounts of pine-dominated ecosystems describe an open savanna-like structure, with low pine density and grass-dominated groundcover (Frost 1993, Lafon 2010). Intact native pine ecosystems in the southeastern U.S. have been reduced and fragmented due to urban development and agriculture (Frost 1993, Duncan and Schmalzer 2004, Lafon 2010), or degraded as the result of fire exclusion (Means 1996, Platt 1999, Stambaugh et al. 2002, Gilliam and Platt 2006).

Increased woody stem densities can alter the community structure and composition, future fire behavior, and ecosystem processes. When fires are infrequent, or excluded, woody stem size and number increase, and woody species can gain dominance and reduce herbaceous species (Waldrop et al. 1992, Scholes and Archer 1997, Haywood et al. 2001, Glitzenstein et al. 2012). A reduction in herbaceous cover, which carries low intensity fires across the landscape, can lead to conditions under which fires are unlikely to spread. Increased hardwood leaf litter can alter decomposition rates and nutrient cycles (Varner et al. 2005, Phillips and Waldrop 2008). Dominance of woody species can also effect pine regeneration, which in southeastern

communities is dependent upon gaps and open ground created by fire (Platt et al. 1988, Gilliam and Platt 1999, Cain and Shelton 2000). Applying prescribed fires to pine-dominated ecosystems can maintain an open structure by reducing hardwood size and number, while having the additional benefits of promoting herbaceous species, allowing for pine regeneration, improving wildlife habitat, and reducing hazardous fuel loads.

Prescribed fire characteristics and fire effects on hardwoods

Fire characteristics (e.g., fireline intensity, flaming residence time, heat released per unit area) are influenced by the time since previous fire, season of burn, weather conditions, and ignition technique. With a greater length of time between fires, increased fuel loads (Williams et al. 1999, Govender et al. 2006, Robertson and Ostertag 2007) can potentially release more energy through combustion (Whelan 1995). In the growing season, the intensity and spread of fires can be dampened by increased relative humidity, greater live fuel moisture content, and a greater proportion of live fuels (Byram 1959, Sparks et al. 2002). Nevertheless, there are observations of increased fireline intensity in the growing season (Glitzenstein et al. 1995), and drought conditions in the spring and summer can lead to wildfires with greater spread (Slocum et al. 2010). Ignition techniques, specifically whether fires are lit so that the flaming front moves with the wind (head fire) or against it (backing fire), produce differences in fire characteristics. Head fires have greater rates of spread, flame lengths, and fireline intensities than backing fires (Beaufait 1965, Wade and Lunsford 1989), and head fires are typically associated with greater scorch of aboveground tissues.

Broadleaf woody species in southeastern pine ecosystems (hereafter hardwoods) are capable of resprouting following fire, but the characteristics of a given fire may influence the post-fire response. Resprouting stems can be formed from a root crown at the base of the plant or

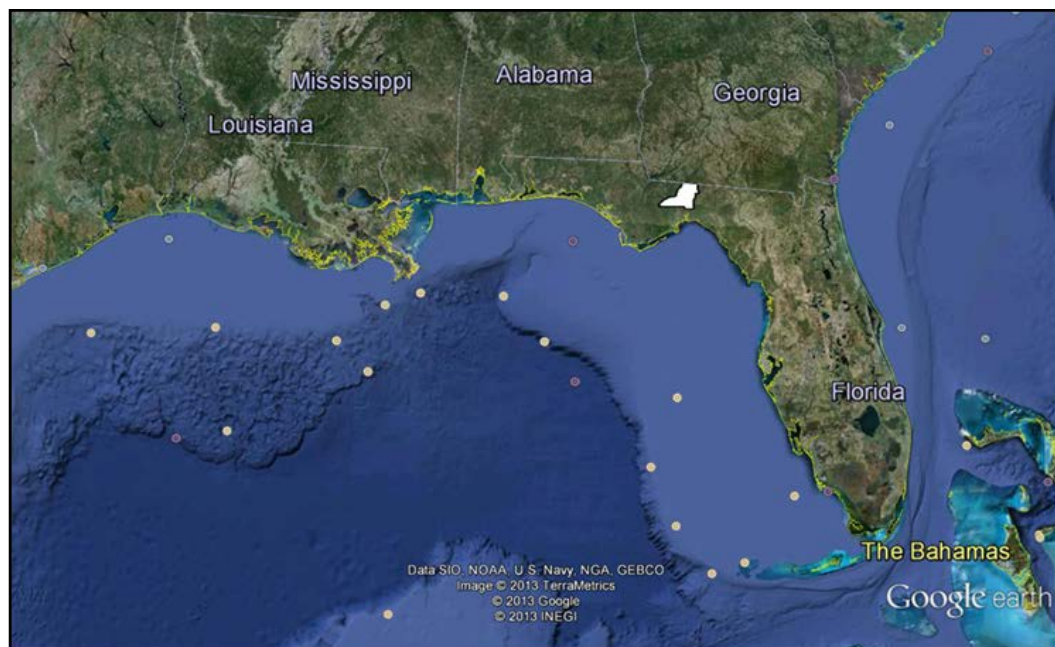
from root suckers (del Tredici 2001). The resprouting stems of hardwoods may be reduced when plants are exposed to greater heat release associated with high fuel loads (Thaxton and Platt 2006, Moreira et al. 2008). Head and backing fires may have different ecological effects related to spatial patterns of combustion. Heat release of volatilized gasses of head fires may be concentrated above the soil surface, leading to lower total fuel consumption and a reduction of total heat energy released. Backing fires may demonstrate greater heating of the soil surface, where resprouting structures are located (Lindenmuth and Byram 1948), which may cause greater damage to genets (Gagnon et al. 2010).

The root reserves available for resprouting at the time a genet is topkilled can also influence growth rates of hardwood resprouts. Woody species in savanna ecosystems may retain larger root reserves in spite of topkilling events, such that individuals can have rapid recovery post fire and persist on the landscape (Schutz et al. 2009, Hoffman et al. 2009, Werner and Prior 2013). In southeastern pine dominated ecosystems resources are stored belowground in hardwood root structures during the dormant season, and these resources can be mobilized for growth and development in the early growing season (Woods et al. 1959). The greater reduction of hardwood size or biomass associated with growing season prescribed fire treatments is attributable to these fires occurring when hardwood resource reserves are reduced (Jones and Laud 1960, Robbins and Myers 1992, Glitzenstein et al. 1995).

Description of Study Site

I conducted my dissertation research at Tall Timbers Research Station (30°35' N, 84°20' W). Tall Timbers is a 1619 ha property, located north of Tallahassee, Florida, in Leon County (Fig. 1.1). The average annual precipitation in Tallahassee is 1556 mm (Southeast Regional Climate Center). The majority of this precipitation occurs in July, while May and October

A



B



Figure 1.1. A. Map of Florida, with Leon County highlighted. B. Location of Tall Timbers Research Station in Leon County, Florida. Maps were created using Google Earth.

typically have the least rainfall (Chen and Gerber 1990). The average annual high temperature is 26.3 °C and low temperature 13.3 °C, occurring in July and January, respectively (Southeast Regional Climate Center).

Field research plots were located in a frequently burned pine-dominated ecosystem, more specifically a shortleaf pine-oak-hickory woodland. This site is dominated by *P. echinata* (shortleaf pine) with scattered mature *Quercus* and *Carya* species. Vegetation surveys at this site suggest minimal ground disturbance, as indicated by the presence of native groundcover species (Robertson 2011, see Glitzenstein et al. 2012). Land management on Tall Timbers maintains an uneven aged structure with an average basal area of approximately 15 m²/ha (Robertson and Ostertag 2007). Prescribed fires have been applied on a two-year fire return interval in the early growing season (March – May) in recent decades.

Dissertation Objectives

The primary objective of my dissertation was to examine how characteristics of prescribed fires vary in response to time since fire, season, and ignition technique of prescribed fires, and how these differences in fire characteristics influence hardwood resprouting. To address questions related to hardwood resprouting, I first needed to establish how specific fire characteristics differ among prescribed fire conditions. Once the effects of prescribed fire treatments on fire characteristics were determined, I explored the relative effects of fire characteristics compared to the size of hardwood genets at the time of topkill. Additionally, I investigated how the method by which hardwoods are topkilled influences resprouting. On the modern landscape, where prescribed fires and fire surrogates are used to maintain the structure of pine-dominated ecosystems, conservation depends upon understanding the mechanisms that control hardwood resprouting.

An Introduction to the Chapters

The chapters of my dissertation will present results from a field study and a shadehouse experiment. The field study was conducted to determine how fire characteristics and hardwood resprouting respond to the time since fire, season of burn, and ignition technique of prescribed fires conducted in a southeastern pine-dominated ecosystem. Results of the field study are presented in Chapters Two and Three. Chapter Two examines how changes in fuel and environmental conditions associated with time since fire and season of burn influence fire characteristics, and if these differences are consistent between head and backing fires. I measured fuel characteristics, weather during each prescribed fire, and fire characteristics of individual fires. Chapter Three focuses on the resprouting response of hardwood genets burned in the prescribed fires reported in Chapter Two. In Chapter Three, I use path analysis to evaluate a model specifying the effects of prescribed fire treatments, and mediating effects of fire characteristics and genet size, on post-burn biomass of hardwood genets. Chapter Four is a shadehouse experiment conducted using water oak (*Quercus nigra*) saplings to examine how the seasonal timing and method of topkill affect resprouting response and root biomass. I applied burn and clip treatments to groups of water oak saplings at three times throughout the year, and sampled plants one-year post topkill. One-year post-topkill, aboveground and belowground biomass were compared among treatments to determine how method and season of topkill influence aboveground and belowground biomass. In Chapter Five, I develop a conceptual model for resprouting response of hardwoods considering of how fire characteristics and resource allocation vary, as well as how method of topkill influences resprouting, based on the conclusions of the field and shadehouse studies. Finally, I suggest implications for land management activities used to control hardwoods in pine-dominated ecosystems of the

southeastern U.S. and how this research improves understanding of tree-grass dynamics in savanna ecosystems worldwide.

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CHAPTER TWO: EFFECTS OF TIME SINCE FIRE, SEASON, AND IGNITION PATTERNS ON FIRE CHARACTERISTICS IN SHORTLEAF PINE-OAK-HICKORY WOODLANDS

Introduction

Many plant communities in the southeastern United States depend on frequent prescribed fire to maintain ecological integrity and achieve forestry management objectives. Historically, southeastern pine savannas burned every one to three years, ignited by lightning strikes during the transition from dry spring to wet summer conditions (Platt 1999, Huffman 2006, Slocum et al. 2010). These frequencies were altered to some extent following human inhabitation by burning practices of Native Americans and European settlers (Stambaugh et al. 2011), and so it is not possible to discern exact characteristics of historical fire regimes. Currently, prescribed fires are conducted under a wide range of return intervals and seasonal conditions in the remaining native savannas and human-modified habitats derived from these communities (often locally designated as pine grasslands, woodlands, and forests). Such variation in application of prescribed fire results from varying interpretations of historical conditions, as well as differences in management objectives, resource limitations, and weather restrictions.

Varying the timing and technique of application of prescribed fire should result in variation in the characteristics of fires. Fire practitioners select the time since previous fire, season of burn, and ignition pattern of prescribed fires to meet various ecological, forestry, and wildfire mitigation objectives. Within these prescription parameters, fuel load and arrangement change with time since fire and season, and weather conditions vary seasonally (Robertson and Ostertag 2007, Knapp et al. 2009). These changes in fuel and weather, combined with the selected ignition pattern, influence fire characteristics related to total heat release and rate of heat release (Whelan 1995). Identifying how fire characteristics change in relation to the prescribed

fire regime in southeastern pine dominated ecosystems is important for predicting characteristics of fires and their likely effects.

Fire characteristics in frequently burned ecosystems are influenced by characteristics of available fuels. Fuels accumulate with time since previous fire, increasing total amounts of combustible materials and potential amounts of energy released (Whelan 1995, Govender et al. 2006, Thaxton and Platt 2006). Fuel structure also changes over time following fires, as woody plants grow above herbaceous species (Waldrop et al. 1992, Haywood et al. 2001, Glitzenstein et al. 2012). Fireline intensity may be reduced by large amounts of leaf litter from woody species (Williamson and Black 1981), although pine needle litter can offset this effect (Ellair and Platt 2013). Fireline intensity can also be increased when fuel moisture content is low (Williams et al. 1999), while high live fuel moisture content during the growing season can reduced fireline intensity (Sparks et al. 2002). The extent to which fuels change over seasons within a year and over successive years and thus modify fire characteristics has not been studied systematically in frequently burned pine communities.

The ignition pattern of prescribed fires determines fire spread relative to wind direction and thus might influence fire characteristics; however, there have been few studies that compare fire characteristics between head and backing fires. Head fires, which have greater rates of spread, flame lengths, flaming zone depths, and fireline intensities (Beaufait 1965, Wade and Lunsford 1989) are generally assumed to have shorter flaming residence times (Beaufait 1965). Nevertheless, there may not be a significant difference in residence time between head and backing fires, as the effect of increased rate of spread of head fires can be canceled out by the longer depth of the flaming front (Wade and Lunsford 1989). The effects of fire spread on fuel consumption and heat release are also uncertain. Backing fires may have higher fuel

consumption, because the vertical distribution of heat release from combusting gases is more highly concentrated near the ground where most of the fuel lies (Lindenmuth and Byram 1948). Empirical studies have shown fuel consumption of backing fires may be greater than (Beaufait 1965) or equal to head fires (Hough 1969, Reid et al. 2012), suggesting the need for further study.

Current fuel and fire modeling software may be biased by not considering certain fuel characteristics associated with particular fire regimes in southeastern ecosystems. Two common fuel consumption models, FOFEM v5.9 (Keane et al. 2005) and Consume v3.0 (Anderson et al. 2009), are based on limited empirical data from southeastern U.S. pine ecosystems. These models use fixed parameters for consumption of fine fuel and generally over-predict fuel consumption in southeastern habitats (Ottmar et al. 2011, Reid et al. 2012). FOFEM estimates changes in amounts of fuel with time since fire, but it does not predict changes in fuel bulk density and potentially associated variables such as fuel moisture (Reinhardt et al. 1997). The most popular program to model fire behavior is the surface module of BehavePlus (Andrews 2009), which predicts fire characteristics based on fuel load and moisture. BehavePlus is designed to predict maximum rate of spread and fireline intensity for suppression and prescribed fire planning. However, the program does not have specific equations to model backing fire (Rossa and Viegas 2009). Accuracy of future modeling software will be improved by both provision of new empirical data and identification of changes in fuel and fire characteristics associated with particular prescribed fire regimes.

I explored how time since previous fire, fire season, and ignition pattern of prescribed fires influence fire characteristics in a frequently burned shortleaf pine-oak-hickory woodland. I tested three hypotheses. (1) Changes in fire characteristics with increased time since fire will be

more complex than predictions based solely on fuel accumulation. I predicted that fireline intensity will increase with accumulation of fuels, but that increased hardwood leaf litter and greater fuel compaction may limit this effect. (2) Season of prescribed fire will affect fire characteristics. Alternative predictions are that fuels will increase in combustibility in the early growing season because of higher ambient temperatures, or else they will decrease in combustibility in the early growing season because of higher relative humidity and associated higher fine fuel moisture. (3) Fireline intensity will be greater for head fires than backing fires, due to the extension of the flaming front and preheating of fuels observed for head fires, but there will be no difference between head fires and backing fires in residence times, reaction intensities, or consumption of fuels because of similarity in combustion on a per area basis.

I tested these hypotheses using plots in which I measured fuel and weather characteristics at the time of fire. My approach was to set prescribed fires with different times since previous fire, in the dormant and growing seasons, with head and backing ignition patterns. I measured fire characteristics associated with each fire and evaluated the differences in fire characteristics associated with prescribed fire treatments. The study produced field measurements of fire characteristics associated with a range of variation in prescribed fire regimes of southeastern pine ecosystems.

Methods

Site Description

This study was conducted at Tall Timbers Research Station (TTRS; 30° 35' N, 84° 20' W), located ~30 km north of Tallahassee (Leon County, Florida, U.S.A.). Soils are well drained loamy fine sands and sandy loams (Paleudults and Kandiudults) (Soil Survey Staff 2012). This area of north Florida is characterized by average high and low temperatures of 26.3 °C and 13.3 °C, and annual precipitation of 1556 mm (Southeast Regional Climate Center). Rainfall peaks in

March and July, while May and November are typically dry (Chen and Gerber 1990). Research plots were established at six sites, which consisted of burn units or pairs of burn units with different fire histories (Fig 2.1), in frequently burned shortleaf pine-oak-hickory woodlands. These second-growth woodlands are dominated by shortleaf pine (*Pinus echinata*) with scattered mature oaks (*Quercus* spp.) and hickories (*Carya* spp.). The groundcover is believed to be native (never plowed) and contains grasses, forbs, and resprouts of hardwood (non-pine) species. These burn units have been managed in recent years with prescribed fire on a two year fire return interval and single tree selection timber harvests maintaining an average pine basal area of ~8 m²/ha (Unpublished data).

Prescribed Fire Application and Measurements

Research plots were established in the spring of 2009. The plots were roughly square, with an area ranging from 10 m x 10 m (0.01 ha) to 15 m x 15 m (0.225 ha). I established plots in sites that had been burned either the previous year (Fig. 2.1; Sites 2, 3, and 5) or two years prior (Fig. 2.1; Sites 1, 4, 6). Mowed and raked fire breaks were established around plots to contain prescribed fires. Prescribed fires were applied from 2009-2011 in a three-way full factorial 2x2x4 design that included two levels of prescribed fire season (late dormant season [January-February] and early growing season [April-May]), four levels of time since fire interval (1-yr, 2-yr, 3-yr, 4-yr), and two levels of ignition pattern (head fire and backing fire), for a total of 16 treatment combinations. One-year and 2-yr time since fire treatment levels were applied in both 2009 and 2010, depending on time since fire at the time of plot establishment. I burned 128 plots, and had 3-14 replicate plots within each treatment combination (Table 2.1). The number of replicates varied due to incomplete burns in certain experimental plots, loss of plots due to land management activities, and unexpected changes in wind direction during fires.

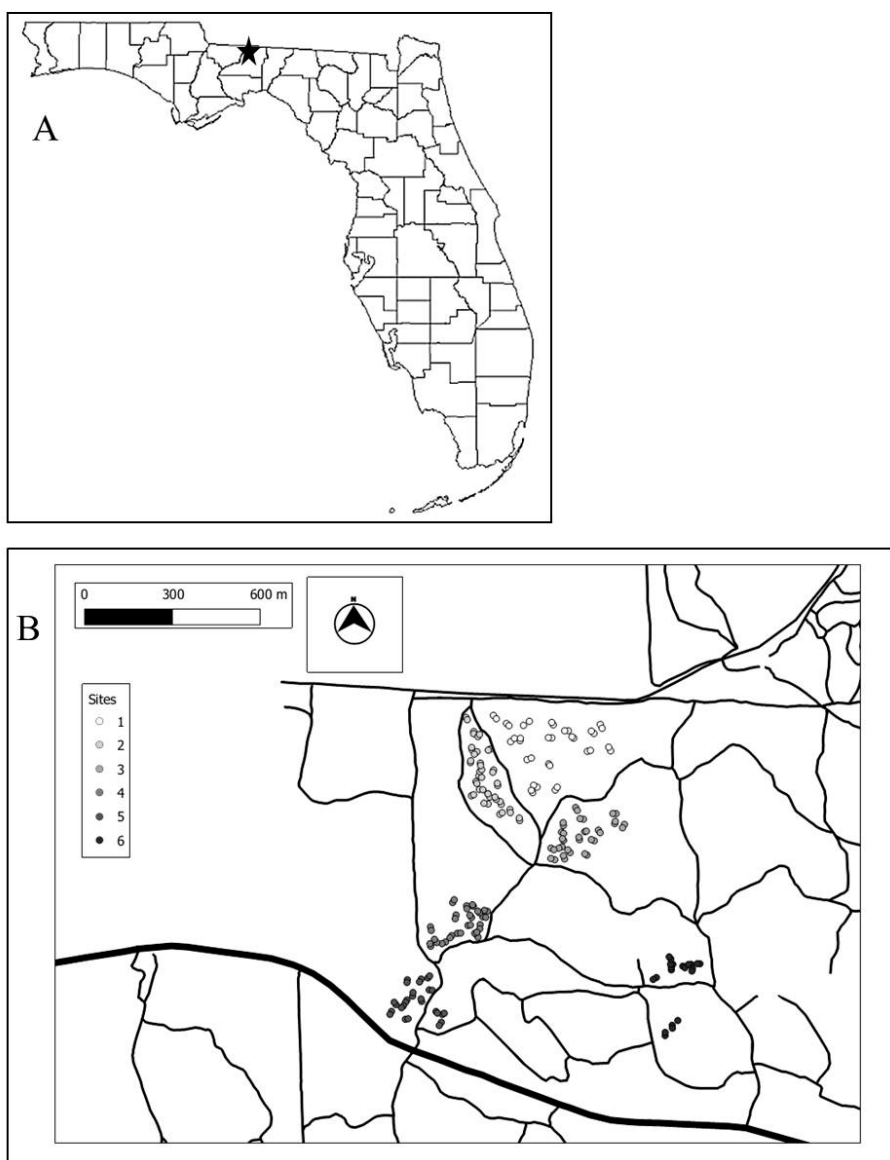


Figure 2.1 (A) Map of Florida, star shows location of Tall Timbers Research Station within Leon County, Florida. (B) View of plot locations on Tall Timbers Research Station. Shaded circles, color coded by site (1-6), represent individual research plots.

Table 2.1. Number of replicate plots (total n=128) within each treatment combination of time since previous fire (1-4 years), burn season (dormant and growing), and ignition technique (head or backing fires).

Ignition technique	Dormant season (January-February)		Growing season (April-May)	
	Head fire	Backing fire	Head fire	Backing fire
1-yr Time since fire	5	3	4	3
2-yr Time since fire	13	14	12	12
3-yr Time since fire	6	6	8	8
4-yr Time since fire	9	9	8	8

Fuel and soil samples were collected from each plot immediately prior to each burn to determine fuel loading and moisture content. Pre-fire fuel samples were collected from three randomly located 0.09 m² (30 cm x 30 cm) quadrats within each plot. All one-hour fuels (≤ 0.6 cm thickness and fine litter) and live herbaceous fuels were collected, as these fuels composed the majority of the available fuel and drive the fire behavior in this community type (Robertson and Ostertag 2007). There was little or no duff (decomposing fine litter) present on these sites due to prior frequent burning. Samples were sealed in plastic bags, brought to the lab and weighed, dried to constant mass in a drying oven at 80 °C, then weighed again to determine both dry biomass and water content (ratio of water to biomass) of each sample at the time of burning. The average fuel bed height of horizontally continuous fine fuels was measured to the nearest centimeter at three points within each plot. Three soil samples (2 cm diameter core, 5 cm depth) were collected from each plot to determine local soil moisture. Soil samples were stored in sealed plastic bags and weighed in the lab prior to oven drying for a minimum of 24 hours at 80 °C, then weighed again to determine water content. After each plot was burned, I collected post-fire fuel samples from three 0.09 m² quadrats located adjacent to pre-fire fuel collections. Post-fire samples were separated into unburned one-hour and live herbaceous fuels, which were oven dried and weighed to estimate fuel consumption.

I burned individual plots as either backing fires or head fires. To apply backing fire treatments, I ignited the downwind fire break edge and allowed the fire to burn through the plot, containing the fire using water and hand tools. To apply head fires, I first used a backing fire to burn out a 2-3 m wide blackline along the downwind edge of the experimental plot and extinguished the fire before igniting a head fire on the upwind edge of the plot and allowing it to burn through the plot into the blackline. This approach allowed us to record the fire

characteristics of a flaming front that was not influenced by flanking or backing fires in close proximity, thus mimicking a segment of a larger fire. Burn prescriptions were typical of prescribed burns conducted in the region, requiring relative humidity between 20-40%, air temperature below 32 °C, wind speeds of 6-12 mph, and that at least one day since last rainfall. This prescription was aimed at providing a complete burn while safely containing fires.

To record temporal patterns of heat release as the flaming front passed I used thermocouple wires attached to data loggers. Thermocouple wires (K-type 0.125 mm diameter, 1 second response time, Omega Engineering Inc.), connected to data loggers (Hobo U12-014, Onset Computer Corporation), were used at three random points in each plot. Thermocouple wire junctions were placed at approximately the mid-point in the height of the fuel bed within the fine fuel matrix (1 cm – 6 cm above the soil surface). Data loggers were placed in a plastic bag and buried at least 5 cm below the soil surface. The maximum temperature of thermocouple wires during fires was considered an index of heat transfer and energy release (Kennard et al. 2005, Bova and Dickinson 2008). Temperatures of thermocouple wires were recorded at 2.0 sec intervals and used to measure flaming residence time (duration of heating > 160 °C) and smoldering residence time (duration of heating > 60 °C). The threshold of 160 °C represented the midpoint of an abrupt transition in temperature between flaming combustion and non-flaming conditions (personal observation), and the 60 °C threshold was used because it is the temperature above which plant tissue is killed (Kennard et al. 2005). At the three points where thermocouple wires were located the average flame length of the passing flaming front was visually estimated to the nearest 10 cm by an observer.

I calculated additional fuel and fire characteristics for each plot from data obtained in the field. Pre-fire fuel samples and fuel bed heights were used to determine fuel bed density (t/m^3).

Adjacent pre- and post-burn samples were used to estimate total fuel consumption (t/ha). Using fuel consumption, residence time, and flame length data, I calculated the following additional fire characteristics: fireline intensity¹ (rate of energy released per unit length of flaming front; kW/m), heat released per unit area² (kJ/m²), and reaction intensity³ (rate of energy released per unit area; kW/m²) (Alexander 1982, Nelson and Adkins 1986, Johnson and Miyanishi 1995). Fire point observations that did not match the assigned ignition treatment (due to wind shifts) were not included in analyses. Fuel measurements and fire characteristics were averaged for each plot. Fuel load and fuel consumption data were included as part of a larger data set reported in Reid et al. (2012).

I used a portable weather station (110-WS-18; Campbell Scientific, Logan, Utah) to monitor and record conditions when each plot was burned. I placed the weather station just upwind of the plot, with sensors located 1.5 m above the ground. Weather data (temperature, relative humidity, wind speed, and wind direction) were collected at five-second intervals and averaged for each one-minute period. These data were used to determine the average weather conditions occurring during each prescribed fire based on ignition and completion times of each plot recorded in the field and confirmed by the recorded temperatures of thermocouples during fires. I also recorded the number of days since last rain and the Keetch-Byram drought index (KBDI) on the days plots were burned, based on data obtained from the permanent weather station at TTRS within 3 km of research plots.

Analysis

I tested for effects of treatments (time since fire, season, ignition pattern) on fuel, weather, and fire characteristics. A multivariate analysis of variance (MANOVA) was run using

¹ Fireline intensity = $258 \times (\text{flame length})^{2.17}$

² Heat per unit area = amount of fuel consumed \times 18,800

³ Reaction intensity = heat per unit area / flaming residence time

time since fire, season, and ignition technique as factors (including combinations), and all fuel and fire characteristics as response variables. I conducted subsequent two-way ANOVAs to determine the effects of time since fire and season of burn on fuel characteristics (fuel height, fuel loads, fuel density, and fuel moisture content), and environmental conditions (air temperature, relative humidity, wind speed, soil moisture, KBDI, days with no rain) individually. To determine the effects of time since fire, season, and ignition pattern on fire characteristics (maximum recorded temperature with fuel matrix, fireline intensity, reaction intensity, flaming and smoldering residence times, heat released per unit area, and percent fuel consumption), and I ran three-way ANOVAs for each of these dependent variables to test for main effects and all possible interactions. Natural log transformations were performed on fireline intensity, reaction intensity, flaming residence time, and smoldering residence time to meet the assumption of normality of the ANOVA. I made pairwise comparisons of all treatment combinations using Tukey-Kramer least-square means tests. All analyses were performed using SAS PROC MIXED (SAS 9.3, SAS Institute Cary, NC) to account for both fixed (experimental treatments) and random (site) effects, with the Kenward-Roger denominator degrees of freedom option due to the unbalanced number of replicates within treatments.

Results

The MANOVA testing for the effects of prescribed fire treatments on fuel and fire characteristics showed that time since fire, season of burn, and ignition technique were significant (Table 2.2). There was also a significant interaction between time since fire and season. This suggests an overall effect of the selected parameters of prescribed fires on both the fuel characteristics and observed fire characteristics in southeastern pine-dominated ecosystems.

Fuel characteristics generally increased with time since fire, with some exceptions. Total fine fuel, represented mainly by one-hour fuels, progressively increased from 1 to 3-yr time since

fire, but decreased slightly from 3 to 4-yr time since fire (Fig. 2.2). Live herbaceous fuel loads increased from 1 to 4-yr since fire, but I observed a reduction in live herbaceous fuel moisture content in the 4-yr plots (Fig. 2.2). One-hour fuel moisture content was also lower in the 4-yr plots compared to 1-3yr plots (Fig. 2.2). In the 4-yr plots only, fuel height decreased and fuel bulk density increased in the growing season compared to the dormant season (Fig. 2.2), resulting in a significant interaction between time since fire and season of burn (Table 2.3).

Table 2.2. Results of MANOVA testing for effects of time since fire (TSF), season of burn (S), ignition technique (I), and all possible combinations of these factors on fuel and fire characteristics.

Factor	Pillai's Trace	ndf, ddf	<i>F</i>	<i>P</i>
Time Since Fire (TSF)	0.8869	39, 270	2.91	< 0.0001
Season of burn (S)	0.7013	13, 88	15.9	< 0.0001
Ignition Technique (I)	0.6781	13, 88	14.26	< 0.0001
TSF * S	0.6010	39, 270	1.73	0.0064
TSF * I	0.2651	39, 270	0.67	0.9334
S * I	0.0914	13, 88	0.68	0.7762
TSF * S * I	0.3342	39, 270	0.87	0.6958

Table 2.3. Effects of time since fire (TSF), season of burn (S), and their interactions on fuel characteristics (total fine fuel, fuel bulk density, fuel depth, and fuel moisture content) indicated by *P* value and *F* value (numerator and denominator degrees of freedom in subscripts). Bold text indicates $p < 0.05$.

		Total fine fuel load	Fuel height	Fuel bulk density	One-hour fuel moisture content	Live herbaceous fuel moisture content
Time since fire (TSF)	<i>P</i>	< 0.0001	0.043	< 0.0001	< 0.0001	0.013
	<i>F</i>	17 _{3, 116}	3 _{3, 50}	8 _{3, 90}	8 _{3, 115}	4 _{3, 120}
Season of burn (S)	<i>P</i>	0.303	0.072	0.018	< 0.0001	< 0.0001
	<i>F</i>	107 _{1, 119}	3 _{1, 115}	6 _{1, 119}	25 _{1, 120}	69 _{1, 120}
TSF * S	<i>P</i>	0.089	0.002	0.007	0.663	0.083
	<i>F</i>	2 _{3, 119}	5 _{3, 100}	4 _{3, 115}	1 _{3, 119}	3 _{3, 115}

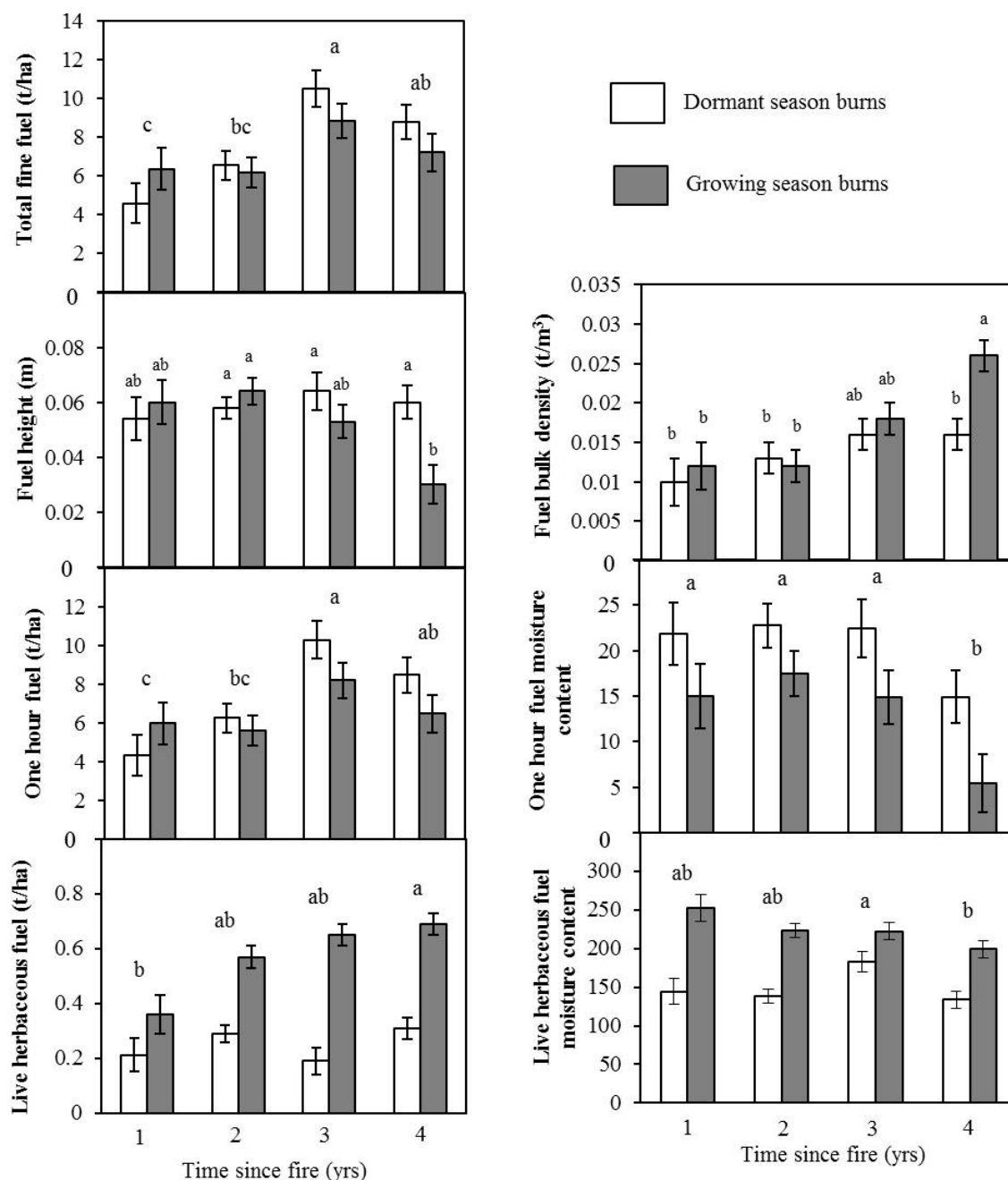


Figure 2.2. Fuel characteristics of plots at the time of prescribed fires. Fuel characteristics (total fuel, fuel height, fuel bulk density, one-hour fuel, one-hour fuel moisture content, live herbaceous fuel, and live herbaceous fuel moisture content) are grouped by time since fire (1 – 4 years) and burn season (dormant, growing). Values are least-square means \pm 1 S.E.. Different letters indicate significant differences among time since fire treatments or time since fire and season combinations where the interaction was significant.

Changes in fire characteristics with increasing time since fire were related to changes in fuel load, fuel moisture, and fuel bulk density. In the 3 and 4-yr time since fire plots, when fuel load was greater and fuel moisture reduced, fireline intensity was approximately four times greater than the 1 and 2-yr plots (Fig. 2.3). This sharp increase between 2 and 3-yr plots was only observed for fireline intensity. Flaming and smoldering residence times and heat per unit area progressively increased from 1 to 4-yr time since fire (Fig. 2.3) reflected by a significant time since fire effect (Table 2.3). While not significant, reaction intensity decreased from the 3-yr to 4-yr time since fire (Fig. 2.3), which corresponded to an increase in fuel bulk density (Fig. 2.2).

Effects of season of burn were limited to fireline intensity and fuel consumption, despite significant differences in weather and fuel conditions between seasons. In the dormant season, I observed lower temperatures, lower relative humidity, higher wind speeds, lower KBDI, and greater soil moisture (Fig 2.4). In addition to these differences in environmental conditions, live herbaceous fuel loads and moisture content were significantly lower in the dormant season across all levels of time since fire (Fig. 2.2). Fireline intensities were greater in the dormant season, but the degree of increase with time since fire differed between seasons (Fig. 2.3). The average increase in fireline intensity from 1 and 2-yr plots to 3 and 4-yr plots was 69.04 kW/m in the dormant season and 24.88 kW/m in the growing season. Percent fine fuel consumption in the 1-yr plots was greater in the dormant season compared to the growing season, but were equal between seasons as time since fire increased (Fig. 2.3), resulting in a significant interaction between time since fire and season for this fire characteristic (Table 2.4). Between the two seasons, there were no significant differences in reaction intensity, residence time, heat per unit area, or maximum thermocouple temperature (Fig. 2.3).

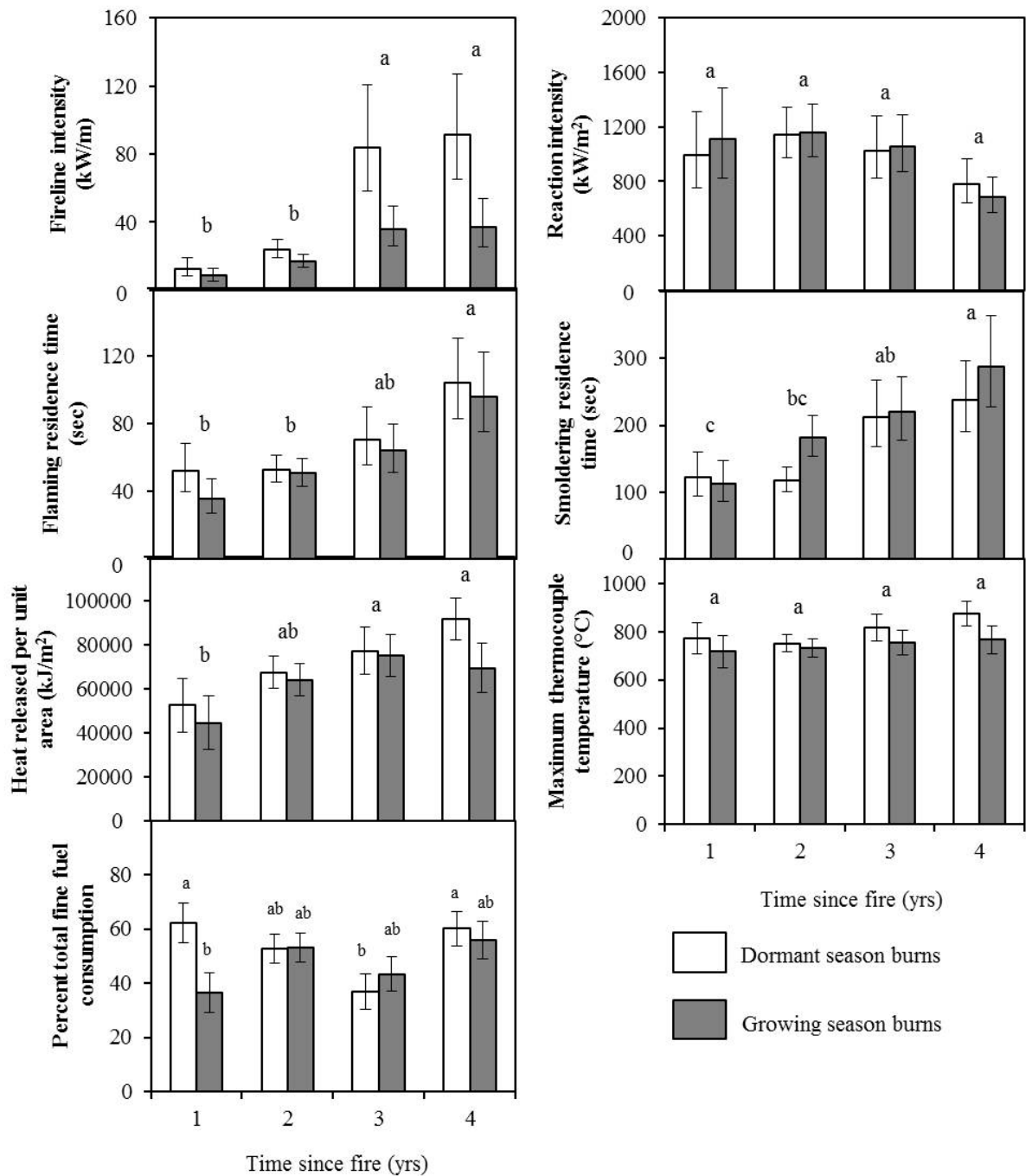


Figure 2.3. Fire characteristics (fireline intensity, reaction intensity, flaming and smoldering residence times, heat released per unit area, maximum thermocouple temperature, and percent total fine fuel consumption) in plots grouped by time since fire (1 – 4 years) and burn season (dormant, growing). Values are least-square means \pm 1 S.E. (back-transformed for fireline intensity, reaction intensity, flaming residence time, and smoldering residence time). Letters indicate significant differences among least-squares means for time since fire treatments or time since fire and season treatment combinations where the interaction was significant.

Table 2.4. Effects of time since fire (TSF), season (S), ignition technique (I) and their interactions on fire characteristics (maximum thermocouple temperature, fireline intensity, reaction intensity, flaming and smoldering residence time, heat release per unit area, and percent fine fuel consumption) indicated by *P* value and *F* value (numerator and denominator degrees of freedom in subscripts). Bold text indicates $p < 0.05$.

		Maximum thermocouple temperature	Fireline intensity	Reaction intensity	Flaming residence time	Smoldering residence time	Heat release per unit area	Percent fuel consumption
TSF	<i>P</i>	0.299	< 0.0001	0.0984	0.001	< 0.0001	0.003	0.013
	<i>F</i>	1.29 _{3, 26}	14 _{3, 22}	2.15 _{3, 101}	6.52 _{3, 51}	8.64 _{3, 81}	5.14 _{3, 69}	3.77 _{3, 103}
S	<i>P</i>	0.070	0.004	0.965	0.280	0.239	0.123	0.032
	<i>F</i>	3.35 _{1, 96}	8.68 _{1, 95}	0 _{1, 101}	1.18 _{1, 102}	1.40 _{1, 104}	2.42 _{1, 109}	4.70 _{1, 107}
I	<i>P</i>	0.937	< 0.0001	0.225	0.806	0.739	0.070	0.018
	<i>F</i>	0.01 _{1, 100}	164.00 _{1, 98}	1.49 _{1, 101}	0.06 _{1, 99}	0.11 _{1, 99}	3.36 _{1, 105}	5.79 _{1, 103}
TSF * S	<i>P</i>	0.775	0.669	0.961	.0913	0.446	0.497	0.009
	<i>F</i>	0.37 _{3, 70}	0.52 _{3, 66}	0.10 _{3, 101}	0.18 _{3, 89}	0.90 _{3, 100}	0.80 _{3, 99}	4.01 _{3, 107}
TSF * I	<i>P</i>	0.748	0.237	0.689	0.308	0.515	0.643	0.434
	<i>F</i>	0.41 _{3, 100}	1.44 _{3, 98}	0.49 _{3, 101}	1.22 _{3, 99}	0.77 _{3, 99}	0.56 _{3, 105}	0.92 _{3, 103}
S * I	<i>P</i>	0.696	0.224	0.077	0.202	0.368	0.286	0.214
	<i>F</i>	0.15 _{1, 100}	1.50 _{1, 98}	3.18 _{1, 101}	1.65 _{2, 99}	0.82 _{1, 98.9}	1.15 _{1, 105}	1.56 _{1, 103}
TSF * S * I	<i>P</i>	0.526	0.839	0.962	0.716	0.514	0.345	0.250
	<i>F</i>	0.75 _{3, 100}	0.28 _{3, 99}	0.10 _{3, 101}	0.45 _{3, 99}	0.77 _{3, 99}	1.12 _{3, 105}	1.39 _{3, 103}

Compared to backing fires, head fires had higher fireline intensity, as predicted, and also resulted in lower percent fine fuel consumption. Average fireline intensities observed for backing fires were less than 20 kW/m, whereas average fireline intensities for head fires were greater than 200 kW/m in 3 and 4-yr plots (Fig. 2.5). Overall, backing fires consumed 6.31% more fine fuel than head fires, and fuel consumption of backing fires was greater for all time since fire levels of treatment (Fig. 2.5). Heat released per unit area, a function of total fine fuel consumption, was also greater for backing fires, although this result was not significant (Table 2.4). The effect of time since fire was consistent for the two ignition patterns (Fig. 2.5), but there was no effect of ignition pattern on reaction intensity, residence times, or maximum thermocouple temperatures (Table 2.4).

Model predictions did not match observed variables when fuel characteristics were used in BehavePlus. The output variables of fireline intensity, reaction intensity, and heat per unit area increased with time since fire, and fireline intensity was greater in the early growing season (Table 2.3).

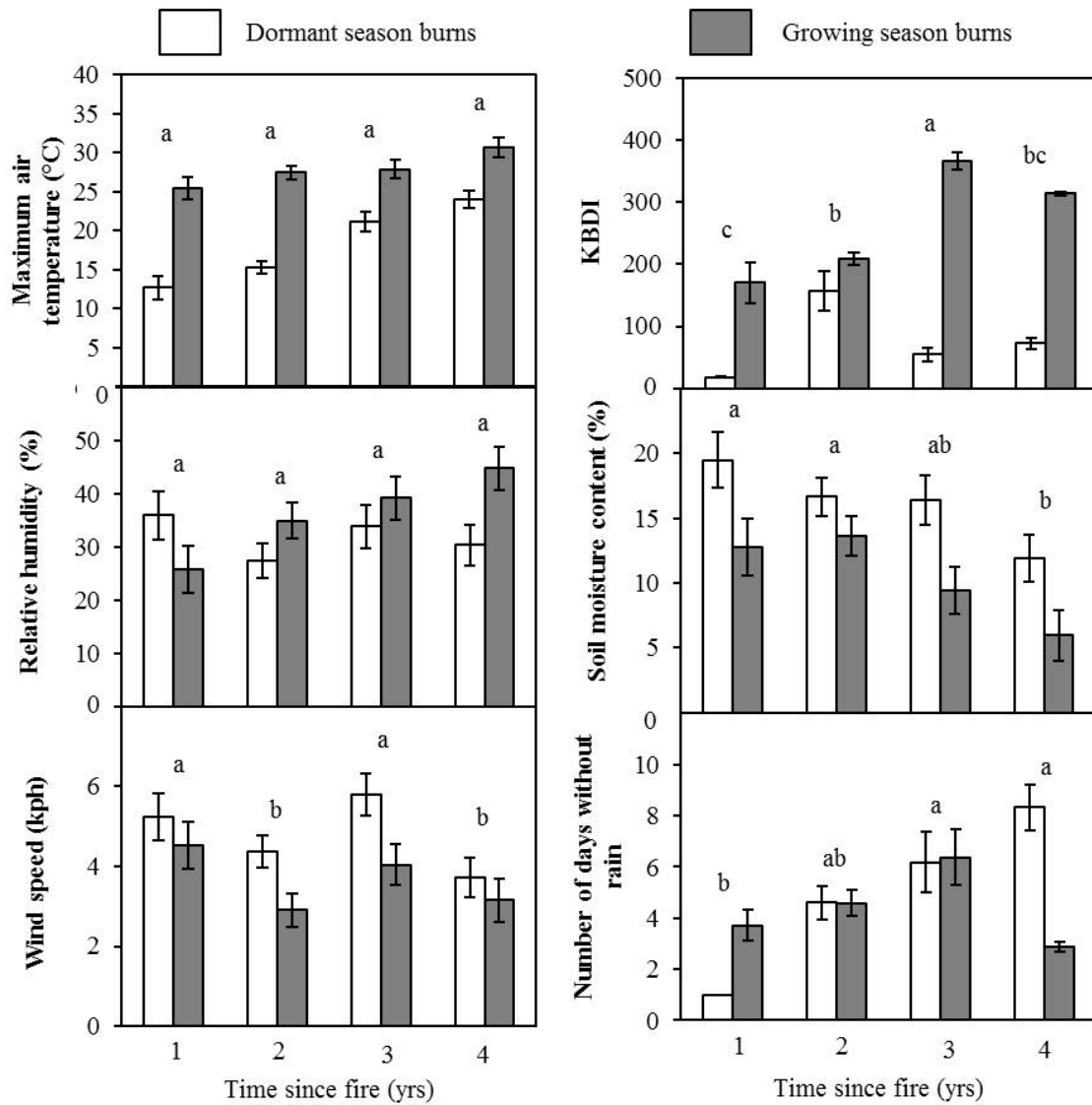


Figure 2.4. Environmental conditions during prescribed fires in plots grouped by time since fire (1 – 4 years) and burn season (dormant, growing). Left: Weather conditions (maximum temperature, relative humidity, and wind speed). Right: Keech-Byram drought index (KBDI), plot soil moisture, and number of days without rain prior to fire. Values are least-square means \pm 1 S.E., and letters indicate significant differences among time since fire treatments.

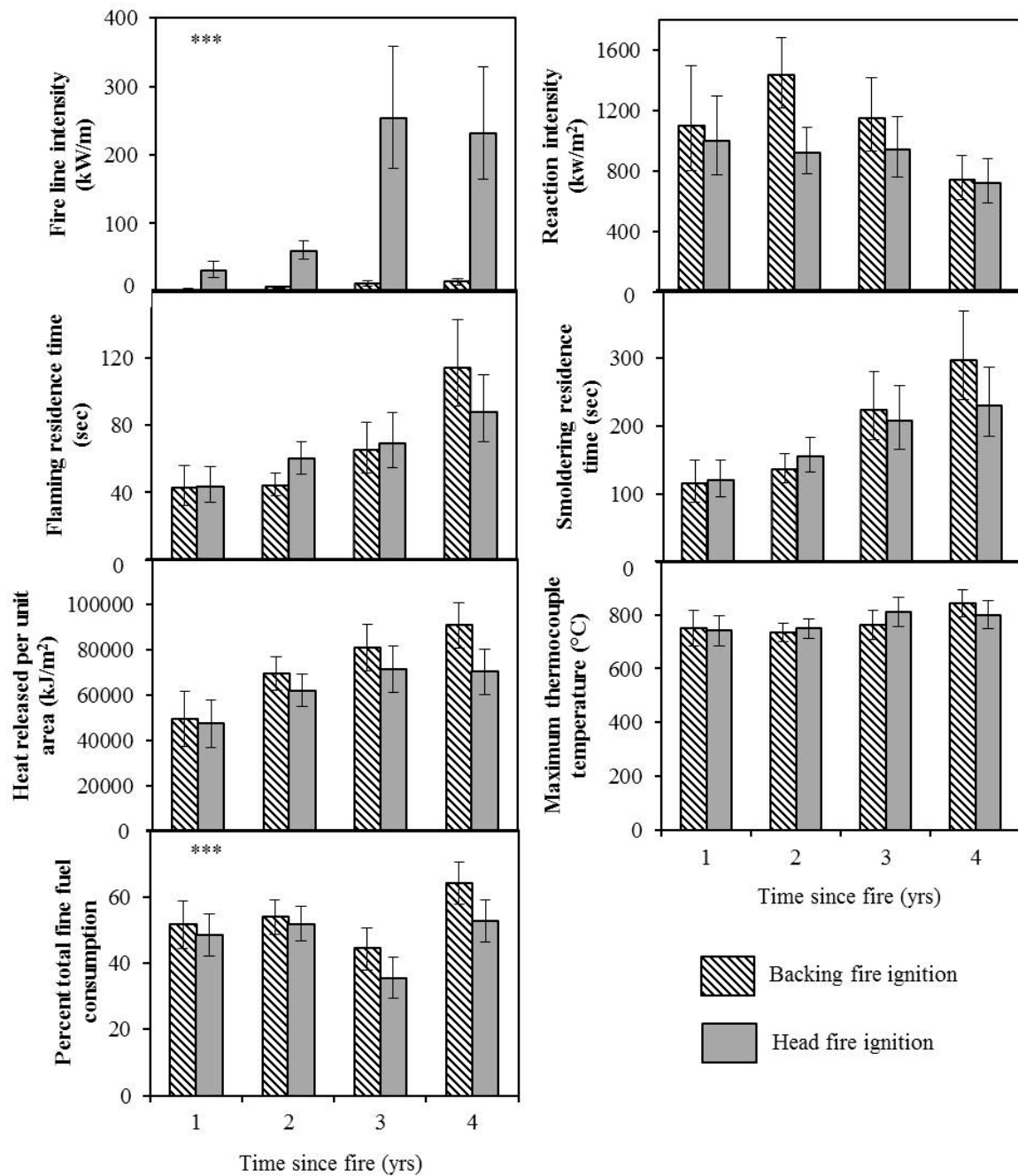


Figure 2.5. Fire characteristics (fireline intensity, reaction intensity, flaming and smoldering residence times, heat released per unit area, maximum thermocouple temperature, and percent total fine fuel consumption) in plots grouped by time since fire (1 – 4 years) and ignition pattern (head and backing). Values are least-square means ± 1 S.E. (back-transformed for fireline intensity, reaction intensity, flaming residence time, and smoldering residence time). Starred (***) panels indicate significant differences between ignition patterns; there were no significant differences for the interaction between time since fire and ignition pattern treatments.

Table 2.4. Predicted and observed values for fireline intensity, reaction intensity, and heat per unit area for the dormant and early growing season with time since fire intervals (TSF) ranging from 1-yr to 4-yrs. Predicted values calculated from BehavePlus surface module using observed fuel moisture characteristics run using standard BehavePlus fuel models 2 and 7.

TSF	Dormant			Early Growing		
	Fireline intensity (kW/m)		Reaction intensity (kW/m ²)	Fireline intensity (kW/m)		Reaction intensity (kW/m ²)
	Predicted	Observed	Predicted	Observed	Predicted	Observed
1	270	12.79	323	993.07	4793	52494
2	263	23.69	321	1142.87	4762	67492
3	265	83.72	322	1025.16	4773	77247
4	320	91.12	336	782.82	4990	91847

Discussion

The changes in fire characteristics associated with time since fire support my hypothesis that the relationship between fire characteristics and fuel are more complex than predictions of increased fuel over time. The observed maximum in fine fuel loading in the 3-yr plots could be because fuels initially accumulate at a rate faster than fuels decompose, after which decomposition catches up with accumulation (Whelan 1995). Precipitation in the years preceding fires can influence fine fuel accumulation (Govender et al. 2006), but given that the 3 and 4-yr plots were all burned in 2011 it is unlikely that this difference in fuel loads was the result of variation in precipitation. A similar peak in fuel loads was observed in South African savannas (Govender et al. 2006), which was matched by a peak in fireline intensity.

I did not observe a difference in fireline intensity between the 3 and 4-yr plots, which may be the result of these plots being burned at a time when fuel and soil moisture was reduced. The lower fuel and soil moisture in the 3 and 4-yr plots is attributable to rainfall being 248.7 mm below average in Tallahassee, Florida and 156.2 mm below average in Thomasville, Georgia (approximately 30 km north of TTRS; Southeast Regional Climate Center) for the months of January through May 2011. The potential effects of low precipitation on fuel moisture and fire characteristics for plots burned in 2011 demonstrates how drought conditions can influence fire behavior.

The apparent relationship between reaction intensity and fuel bulk density reveals further complexity in the association between fuel and fire characteristics. Reaction intensity decreases with greater fuel bulk density because of lower oxygen availability (Whelan 1995, van Wagtendonk 2006), which slows the rate of energy release. Differences in fuel bulk density and fuel height between seasons in the 4-yr plots may be due to an increase in the proportion of hardwood leaf litter. As new leaf growth is initiated in the spring, and leaves from the previous

growing season are shed, the input of leaf litter may cause greater fuel compaction. Decreased reaction intensity as fuel compaction increases has also been observed in native longleaf pine communities (Robertson and Ostertag 2007).

These data support my prediction that greater fuel moisture and relative humidity in the growing season would reduce combustibility of fuels. Increased live herbaceous fuel load and moisture content in the growing season likely limited fireline intensity, due to increased fuel moisture requiring more energy to heat fuels to the point of combustion (Byram 1959). Similar to my observations, a study at a shortleaf pine site in Arkansas found fireline intensity to be 1020 kW/m lower during growing season fires (September) compared to dormant season fires (March and April) (Sparks et al. 2002). This finding contrasts with that of a study conducted in a longleaf pine community where fireline intensity increased throughout the growing season (Glitzenstein et al. 1995). Observations of increased fireline intensity in the growing season may be attributed to drying trends in fuels prior to onset of the rainy season (Slocum et al. 2003, Slocum et al. 2010). Had my seasonal treatments extended, such that fires were conducted under seasonally dry conditions, then I may have observed increased fireline intensity compared to the early growing season fires.

Although, head fires had the expected higher fireline intensity than backing fires the result of higher fuel consumption by backing fires contradicted my hypothesis that there would be no effect of ignition pattern on the other fire characteristics. While head fires have greater intensity and severity, reaction intensity did not differ between ignition patterns, suggesting that the overall heat energy release between head and backing fires is very similar in these ecosystems (Wade and Lundsford 1989). The difference in fuel consumption may be related to the lower vertical concentration of combustion of volatiles during backing fires (Lindenmuth and

Byram 1948), or else head fires being “oxygen starved” near the ground, making head fires less efficient at combustion and oxidation of fine fuels (Lobert and Warnatz 1993).

The lack of effect of treatments on maximum thermocouple temperature demonstrates that maximum temperatures may reveal little about other characteristics of fires. Maximum temperature within a flame will be similar regardless of fire characteristics (Van Wagner and Methven 1978), and devices placed within the flaming zone typically under-predict the air temperature in the flame zone (Kennard et al. 2005). Variables that reflect the duration of heating or heat energy release (residence time, fireline intensity, reaction intensity, heat release per unit area) are more important for evaluating and comparing fire characteristics and ecological effects (Rothermel and Deeming 1980, Johnson and Miyanishi 1995).

Results from this empirical study show patterns of interest in both fuel and fire characteristics that current fuel and fire models do not necessarily incorporate or predict. I observed fuel characteristics for all levels of the time since fire treatment differ from those predicted by FOFEM (loblolly shortleaf pine model), in which litter fuel decreases following the first year after fire, duff (which was minimal at my study sites) increases, and herbaceous fuels are considered absent (Reid et al. 2012). Predicted fire characteristics in BehavePlus were also different from field observations. The decrease in reaction intensity despite increased fuel consumption is not predicted by BehavePlus, which predicts higher reaction intensities with increases in fuel load, although such increases appear mediated by bulk density. Further, given the potentially important effect of ignition pattern documented in this study, the current BehavePlus model is limited in that it does not specifically model behavior of backing fires.

The results of my study provide insight on how prescribed fire regimes and associated fire characteristics in frequently burned pine ecosystems may influence vegetation dynamics.

The greater fireline intensity, residence times, and heat per unit area associated with higher fuel loads in savanna ecosystems (Williams et al. 1998, Robertson and Ostertag 2007, Ellair and Platt 2013) can reduce resprouting of woody plants (Bova and Dickinson 2005, Thaxton and Platt 2006), although the potential for topkill may decrease as woody plants increase in size (Waldrop et al. 1992). The lower fireline intensity in the growing season, and insignificant effect of season of burn on other fire characteristics, suggests that effects of early growing season burns on woody plants are not related to the direct impact of fire, but rather seasonal variation in above versus belowground allocation of carbohydrates (see Glitzenstein et al. 1995, Knapp et al. 2009). The difference in fireline intensity associated with ignition pattern is not likely to impact herbaceous plants and shrubs, given no measureable differences in the more directly important variables of residence time and reaction intensity.

I observed the time since previous fire treatment to have the greatest effect on expected fire characteristics, but that the intensity of these fires can be mediated by season and ignition patterns. Meeting management objectives related to fireline intensity, such as minimizing crown scorch, may require adjusting ignition patterns or the seasonal of burn as fuel loads increase over time. Offsetting fireline intensity is unlikely to influence fuel consumption, residence time, or heat release per unit area, as these fire characteristics are related to fuel amounts rather than season or ignition pattern. Understanding how fire characteristics are likely to change or not change based on a burn prescription, and being able to predict fire characteristics of ecological importance (Dickinson and Ryan 2010), should improve the ability of fire practitioners to meet land management objectives using prescribed fire.

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CHAPTER THREE: DETERMINING RESPROUTING RESPONSE OF HARDWOOD GENETS TO PRESCRIBED FIRE TREATMENTS USING PATH ANALYSIS

Introduction

Frequent topkill of woody plants by fire is one of the most important processes for maintaining the open structure of savanna ecosystems. Frequent topkill limits the aboveground height and biomass of woody plants, which otherwise have the potential to become dominant in the ecosystem. When woody species become dominant there is typically a loss of herbaceous species and diversity (Scholes and Archer 1997), and the ecosystem can become poor quality habitat for endemic plants and animals. When fires kill aboveground woody plant tissues (i.e. topkill), resprouting stems are formed from dormant buds, or meristems, at the base of the plant. This new growth is supported by energy stored in the roots (Bowen and Pate 1993, El Omari et al. 2003). Determining how fire characteristics and timing of fires influence resprouting can be difficult, as both fire characteristics and root reserves of plants change depending upon the conditions selected for prescribed fires.

Resprouting of woody plants can be affected by the time since fire and season of burn. Longer intervals between fires allow hardwoods to accumulate biomass aboveground and stored within roots (Kabeya and Sakai 2005). Plants with larger root reserves at the time of topkill typically have increased growth rates of resprouting stems (Malanson and Trabaud 1988, Schutz et al. 2009). Rate of recovery of aboveground biomass is also influenced by the season of burn. In the transition from the dormant season to the growing season, resources are mobilized from the roots to aboveground structures to support new growth (Woods et al. 1959). When topkill occurs during this seasonal low in root reserves, plants have limited resources available for resprouting, resulting in reduced resprout biomass (Jones and Laud 1960, Robbins and Myers 1992, Landhäusser and Lieffers 2002, Grady and Hoffmann 2012).

Fire characteristics may also influence resprouting as heating at the base of a plant damages dormant buds. The characteristics of fires (e.g., fireline intensity, flaming residence time, fuel consumption) are influenced by the time since fire, season in which the prescribed fire is conducted, and ignition techniques used. Accumulation of fuel loads over time can increase fireline intensity, residence time, and heat released per unit area (Govender et al. 2006, Thaxton and Platt 2006). Greater heat energy released at the base of hardwood genets could lead to increased damage to dormant buds near the soil surface (Moreno and Oechel 1991, Moreira et al. 2008). Greater heating at the base of woody plants can also occur as the result of the ignition technique (i.e., direction of the flaming front in relation to the wind). Head fires, which spread in the same direction as the wind, have greater fireline intensity than backing fires, but the heat released from combusting gases in the convection column within the flaming front of a head fire may be higher off the ground (Lindenmuth and Byram 1948). If heat release of head fires is concentrated above the soil surface, head fires may be less damaging to meristems (Gagnon et al. 2010).

Determining if the observed resprouting response of hardwoods is associated with fire characteristics or genet resource allocation when conducting studies in natural systems can be complicated. Previous studies investigating how seasonal changes in resource allocation or fire intensity influence hardwood resprouting found support for effects of both plant physiology and fire intensity on stem density (Drewa et al. 2002, 2006). Determining the strength of these effects requires evaluating the system as a whole, where fire characteristics are a mediating factor (Fig. 3.1). For example, season of burn can have a direct effect on growth rate of hardwood resprouts if topkill occurs when root reserves are reduced, but these effects may also be mediated by fire characteristics related to the season of burn (e.g., reduced resprout size associated with greater

heating at the base of the plant). Improved understanding of the mechanisms controlling hardwood resprouting response to fire will lead to greater understanding of the balance between woody and herbaceous species in savanna ecosystems and allow land managers to control hardwoods.

To evaluate the effects of experimental prescribed fire treatments on hardwood resprouting, taking into account changes in fuels, fire, and pre-burn size of hardwood genets, I used path analysis. Path analysis, a component of structural equation modeling (SEM), has an advantage over univariate methods (i.e., methods that analyze one dependent variable) in evaluating ecological systems (Grace 2006). SEMs allow for variables to simultaneously act as a response to treatments and to have effects on other dependent variables. Modeling the interactions as a network of effects can evaluate mechanisms with mediating factors.

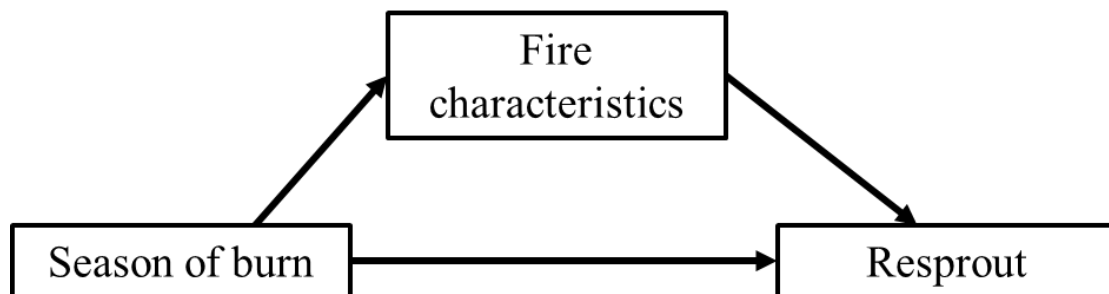


Figure 3.1. Example of a mediation model. Season of burn can have a direct effect on hardwood resprouts or be mediated via fire characteristics.

In this chapter, I first build a conceptual model showing the expected relationships among fire characteristics and hardwood resprouting based on existing knowledge of fire ecology of savanna ecosystems. From this conceptual model I develop a path analysis model to identify relationships among prescribed fire treatments (specifically: time since fire, season of burn, and

ignition technique), fuel characteristics (e.g., total fine fuel load, fuel bulk density), environmental conditions (e.g., relative humidity, KBDI), fire characteristics (e.g., fireline intensity, residence time), and resprouting of hardwood species (e.g., stem height, aboveground biomass) in a southeastern pine-dominated ecosystem. I used this method to explore two non-mutually exclusive hypotheses: (1) The effects of prescribed fire treatments on hardwood resprouting response are mediated by the size of the plant at the time of topkill, such that larger genets at the time of topkill will have a greater size post-burn. (2) The effects of prescribed fire treatments on hardwood resprouting response are mediated through fuel and fire characteristics, such that fires conducted under conditions that result in greater heating of genet meristems will reduce the size of resprouting genets. Determining how fire characteristics and hardwood resource allocation influence the resprouting response of hardwoods based on the time since fire, season, and ignition technique of prescribed burns is important for the restoration and conservation of these ecosystems using prescribed fire.

Development of conceptual model

I relied on a priori and theoretical knowledge of fire and hardwood resprouting response in savanna ecosystems to develop a conceptual model of the expected relationships between prescribed fire treatments, observed fire and fuel variables, and hardwood genet size. In the conceptual model (Fig. 3.2) each rectangle can represent multiple observed or unobserved variables. The prescribed fire treatments (ignition technique, time since fire, and season of burn) represent experimental treatments applied to the plots in this study (see Chapter 2 for details). Fire characteristics, fuel characteristics, and environmental conditions represent groups of observed variables that vary within the prescribed fire treatments but were not experimentally manipulated.

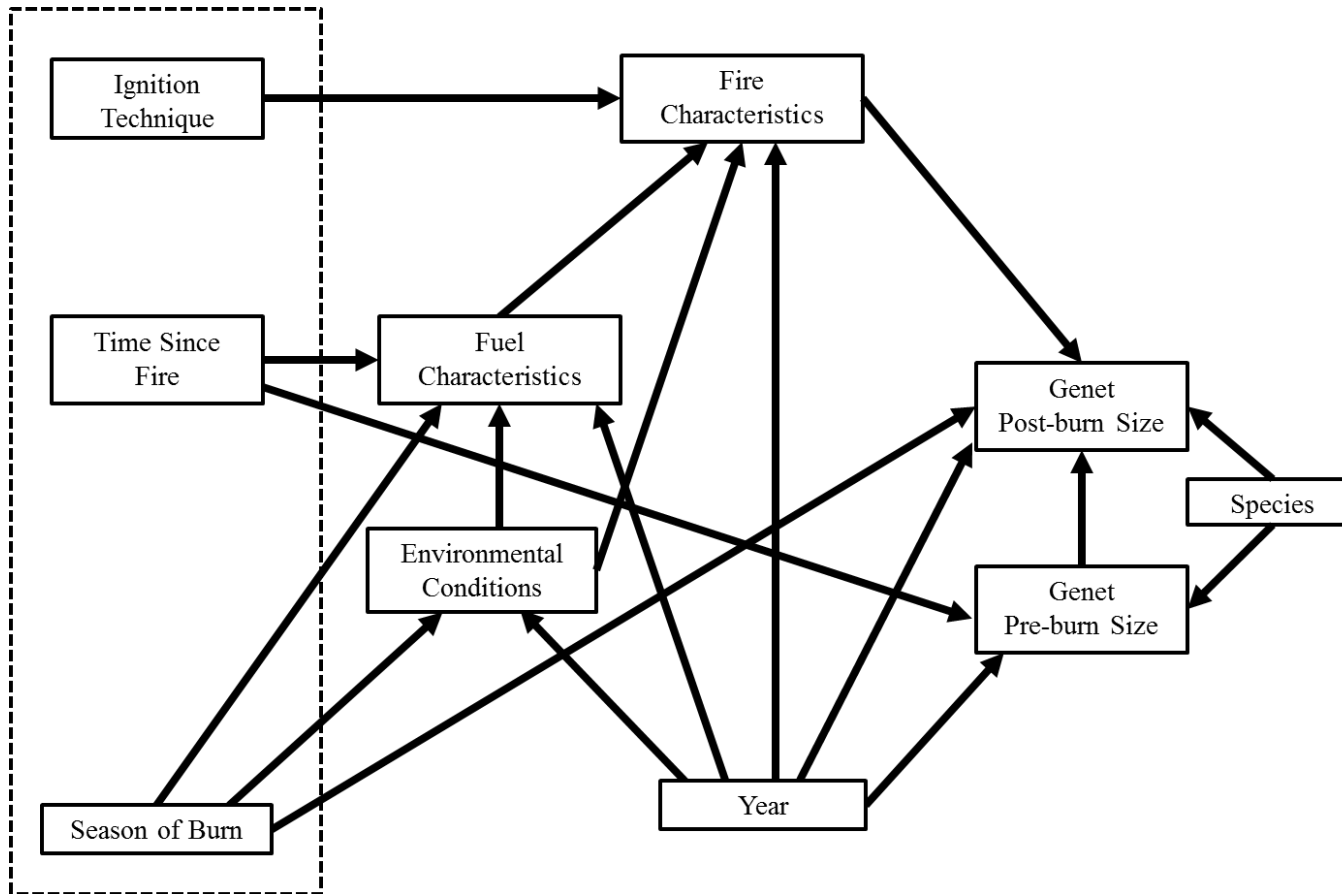


Figure 3.2. Conceptual model describing relationships among prescribed fire conditions (outlined in dashed box), fire characteristics, fuel characteristics, environmental conditions, and pre- and post-burn genet characteristics. Rectangles for prescribed fire conditions represent the experimental treatments for ignition technique (head or backing fire), time since fire (2-yr to 4-yr since previous fire), and season of burn (dormant season or growing season). Rectangles represent groups of variables, including fire characteristics (e.g., fireline intensity, residence time), fuel characteristics (e.g., fuel load, fuel bulk density), environmental conditions (e.g., relative humidity, air temperature, KBDI), pre- and post-burn genet characteristics (e.g., number of stems, stem height, aboveground biomass). Rectangles for species (in this experiment *Q. falcata* and *C. alba*) and year are also included to account for differences in growth rates or response of species and any year-to-year variation that can influence observed variables.

Effects of prescribed fire treatments on the resprouting response of hardwoods may be mediated by characteristics of the fire, and by the size of the plant at the time it is burned. While the two hypotheses consider the combined prescribed fire treatments, the path analysis model enables an evaluation of questions related to individual pathways, including: (1) Is the effect of time since fire on post-burn size mediated through fuel and fire characteristics, or is the effect on resprouting response stronger via the path of pre-burn genet size? As the time since previous fire increases there is an accumulation of fuel, which should have a positive effect on fireline intensity, flaming and smoldering residence times, and heat release per unit area (Whelan 1995, Govender et al. 2006). As fire characteristics such as residence times and heat release per unit area increase, there may be a greater heating of plant tissues resulting in a negative effect on hardwood resprouting response (e.g., fewer stems, reduced growth rate). Conversely, the effect of time since fire on resprouting response is expected to be positive via pre-burn size. Genets accumulate biomass as the time since fire increases, and larger genets typically produce larger resprouts (Malanson and Trabaud 1988, Schutz et al. 2009). (2) Is the effect of season on post-burn size mediated through the pathways of environmental conditions, fuel characteristics, and fire characteristics, or is there a greater direct effect of seasonal changes in resource allocation? In the dormant season, lower relative humidity and smaller quantities of live fuel increase fireline intensity (Chapter 2, Sparks et al. 2002) which can decrease resprout size. However, this greater fireline intensity occurs when hardwoods have larger root reserves, which may counter the effects of high intensity fires. Conversely, fires occurring in the early growing season can have a negative effect on resprout size because root reserves are reduced at this time (Woods et al. 1959). While I did not measure root reserves in this study, I can assume that the direct effect of season of burn on resprouts measured after the fire are attributable to seasonal changes in

resource allocation without having a mediating observed variable for root biomass. (3) Is there an effect of ignition technique on post-burn size via fire characteristics? The concentration of heating and combustion at the ground level, where meristems are located, may be greater for backing fires (Lindenmuth and Byram 1948), resulting in a more negative effect compared to head fires. (4) What is the influence of year-to-year variation on variables and relationships between variables in the model? Year-to-year differences, which cannot be controlled for and may influence the environmental conditions, fuel characteristics, fire characteristics, pre-burn genet size, or post-burn genet size observed within a given year. (5) Is the response of species to topkill similar? Hardwood species may have different sizes within a time since fire treatment or different growth rates post-burn, which could affect genet size before and after burns.

Methods

Plot establishment and prescribed fire application

This study was conducted at Tall Timbers Research Station (30° 35' N, 84° 20' W) located north of Tallahassee, Florida. Prescribed fires were applied to 128 plots in 2009-2011 in a three-way full factorial design. There were two levels of season (late dormant, early growing), four levels of time since fire (1-yr, 2-yr, 3-yr, 4-yr), and two levels of ignition technique (head, backing). The number of replicate plots within each of the 16 treatment combinations ranged from 3-14. A more detailed description of the study site, plot establishment, prescribed fire application, fuel sampling, environmental data collection, and prescribed fire observations are provided in Chapter 2.

Hardwood measurements

When plots were established I selected 10 hardwood genets within each plot. Individual genets were identified as groups of stems appearing to have a shared root stock that were

separate from nearby genets. The majority of genets were in the genera *Quercus* and *Carya*. For each genet, I counted the number of stems, and measured the height and basal diameter for each stem. Each genet was measured 1 to 14 days before its plot was burned. Biomass of each stem in the genet was calculated using allometric equations for each species (Robertson and Ostertag 2009) and biomass was then summed for each genet. Genets were measured one year after burning using the same method.

Data

I took the following steps to prepare the variables describing environmental conditions, fuel characteristics, and fire characteristics: (1) Weather conditions (recorded at one minute intervals during fires), soil moisture (three samples per plot), fuel characteristics (three samples per plot), and fire characteristics (three points per plot) were averaged for each plot. The number of days since previous rainfall and Keech-Byram drought index (KBDI) were single values assigned to plots on the day of burn. (2) I examined the normality of all variables using Shapiro-Wilk tests and histograms in PROC UNIVARIATE (SAS 9.3, SAS Institute, Cary, NC). The frequency distributions of fuel characteristics were improved when square root transformed, and distributions of fire characteristics and KBDI were improved when natural-log transformed. (3) There were missing data for less than 10% of the observations. I filled these missing data with an estimate derived from intact fuel, weather, and fire characteristic values using multiple imputation (PROC MI, SAS 9.3; Rubin 1996). Missing values were filled with 97 - 99% efficiency.

I used the two most common hardwood species, *Quercus falcata* (southern red oak) and *Carya alba* (mockernut hickory), in the evaluation of the model. These two species had the greatest number of observations in the data set (58% of genets sampled) and were the only

species with sufficient sample size for use in the path analysis. Genets included in this analysis were limited to those that met the following criteria: (1) all aboveground tissue was killed in the fire, (2) resprouting occurred from the root collar after the fire, and (3) genets were alive one year after the fire. For the two species used in this analysis, 95% of *Q. falcata* genets and 93% of *C. alba* genets met these criteria. The frequency distributions of pre-burn and post-burn number of stems, stem height, and aboveground biomass were evaluated for normality in the same manner as fuel and fire characteristics. Pre-burn and post-burn biomass values were natural-log transformed to improve the distribution and linearity of the data. Transformed values of pre-burn and post-burn biomass were then averaged across genets within plots. The number of genets within plots ranged from 1-8 for *Q. falcata* and 1-6 for *C. alba*.

The one-year time since fire plots had a very low sample size because of damage to plots and incomplete burns. This reduced the number of replicates to 3-5 per treatment combination. Because of this reduced sample size, I was not able to include the one-year plots in the path analysis.

Development of path model

To develop my path analysis model, I considered the experimental treatments (time since fire, season of burn, ignition technique) and their predicted relationships with observed variables as presented in the conceptual model (Fig. 3.2). I determined which observed variables were most representative of the conceptual variables for inclusion in the path analysis, similar to methods outlined in Grace and Keeley (2006). All of the observed variables within the study could not be included in the analysis, as such analyses require a minimum number of five replicates per parameter estimated (see Lee and Song 2004). It was therefore necessary to

include the observed variables that were most relevant, while still keeping the model informative.

The path analysis included variables representing the experimental prescribed fire treatments applied to plots and observed fuel characteristics, fire characteristics, and hardwood variables within the plots. The prescribed fire treatments were time since previous fire (2-4 years), season of burn (dormant or early growing), and ignition technique (head or backing fire). For fire characteristics, I selected two variables, fireline intensity and heat per unit area, which were uncorrelated ($R^2 = 0.02$). Fireline intensity (rate of energy released per unit length of flaming front; kW/m) is often correlated with indices of fire severity, including damage to aboveground leaves and branches (Whelan 1995, Keeley 2009). Heat released per unit area (kJ/m²) is an indicator of where heat is released in the fine fuel matrix and is most likely to influence the dormant buds of hardwood genets (Bowen and Pate 1993, Schutz et al. 2009). To represent fuel characteristics, I used total fine fuel (i.e., one-hour fuel and live herbaceous fuel), which drives the observed fire characteristics in this ecosystem (Robertson and Ostertag 2007). For environmental conditions I used season to represent changes in environmental variables (e.g., KBDI, soil moisture, relative humidity, temperature) because the environmental variables were different between the two seasons (Table 3.1, see Chapter 2). For genet size, I used pre-burn genet biomass and post-burn genet biomass.

Table 3.1. Average KBDI and weather conditions (wind speed, relative humidity, temperature) for each season. All years (2009, 2010, and 2011) are combined. Values are mean \pm 1 s.e.

Season of burn	KBDI	Wind speed (kph)	Relative humidity (%)	Temperature (°C)
Dormant	91.38 \pm 15.12	4.21 \pm 0.19	29.86 \pm 1.31	19.74 \pm 0.64
Early Growing	281.43 \pm 12.81	3.32 \pm 0.19	37.22 \pm 1.68	27.17 \pm 0.63

Species was included as a dummy variable to control for differences in resprouting response and growth rates between *Q. falcata* and *C. alba*.

The year 2011 was included in the model to account for the low precipitation occurring in 2011 compared to 2009 and 2010. Average annual precipitation in Tallahassee, Florida is 1556 mm (Southeast Regional Climate Center). Annual precipitation in 2009 was 1476 mm and in 2010 was 1487 mm, whereas precipitation in 2011 was 884 mm (672 mm below average). In addition to the drought potentially influencing observed variables, the time since fire treatment and year were confounded, in that all 3-yr and 4-yr time since fire plots were burned in 2011. To address this issue, I included a correlation between these two variables in the model.

Model evaluation

Model estimation was based on maximum likelihood. I evaluated the overall model fit using chi-square and associated *P* values. In evaluation of these models, *P* values of > 0.05 are considered to have acceptable fit (Grace 2006). When a model did not fit, I examined the residual covariances, which indicate deviations from expected covariances between variables in the model. When large deviations are indicated, the model suggests relationships that were not well defined and if added to a new model can improve model fit. While new pathways suggested by these deviations may generate new hypotheses, new pathways should not be added if the suggested pathway is not supported by theory (Grace 2006). All analyses were performed using IBM SPSS Amos version 20 (Arbuckle 2011).

Results

The initial model did not fit the data (chi-square 51.46, $df = 26$, $p = 0.002$). Residual covariances indicated a deviation in the predicted and observed covariance between time since fire and post-burn genet biomass. When I added a correlation between these two variables (grey

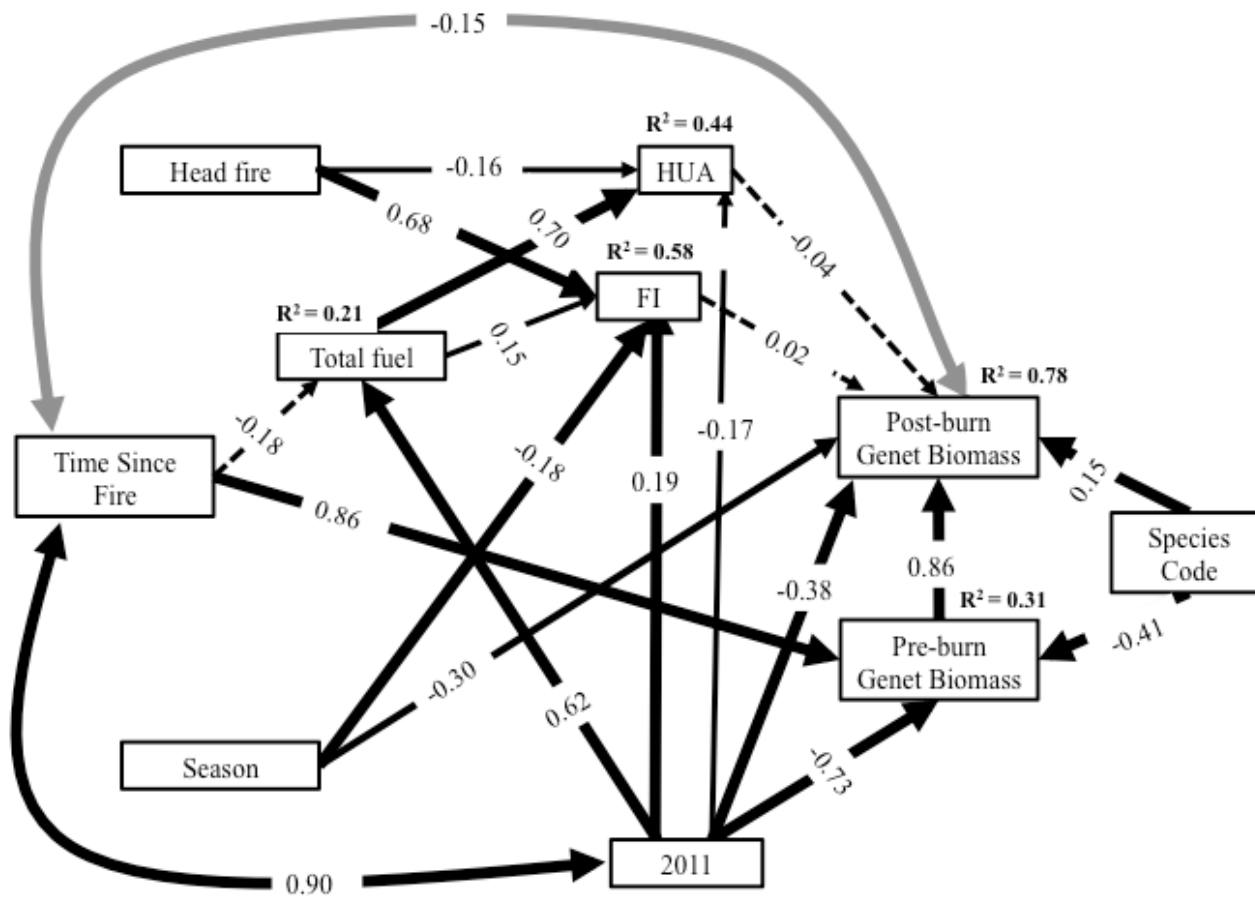


Figure 3.3. Path analysis model (chi-square=27.05, df=25, $p=0.354$) describing relationships among prescribed fire conditions (head fire, time since fire, growing season burns), total fuel, fireline intensity (FI), heat released per unit area (HUA), pre-burn genet biomass, and post-burn genet biomass (one-year post fire), and year (2011). Values on paths are standardized partial regression coefficients. Significance of coefficients is represented by weight of arrows (dashed line = ns, thin arrows = $p \leq 0.05$, thick line = $p \leq 0.0001$). This final path analysis model includes the addition of a correlation between time since fire and 2011 (grey arrow).

arrow, Fig. 3.3), to account for this unresolved correlation, the overall model fit was improved (chi-square of 27.05, $df = 25$, $p = 0.354$). Inclusion of this correlation in the model did not change the significance of the existing paths or my interpretation of the model.

The final model explained 78% of the variation in the post-burn biomass of genets, 58% of the variation in fireline intensity, 44% of the variation in heat released per unit area, and 21% of the variation in total fuel loading (Fig. 3.3). In Figure 3.3, the strength of effects is shown by path coefficients, and significance of the path by the weight of the arrows. The path coefficient values associated with each arrow are standardized partial regression coefficients. These values represent the expected change if a given predictor is varied and all other predictors are held constant.

The model suggests that plots that had not been burned for a longer period of time had larger genets, and that these larger shrubs, in turn, produced larger resprouts after fires. The positive effect of time since fire on pre-burn genet biomass (0.86) shows that genets increased in biomass with time since fire, and the positive effect of pre-burn genet biomass on post-burn genet biomass (0.86), shows that larger genets at the time of topkill produced larger resprouts (Fig. 3.3). The indirect effect (i.e., product of path coefficients) of time since fire on post burn genet biomass ($0.86 \times 0.86 = 0.74$) was also positive. The negative correlation (-0.15) between time since fire and post-burn genet biomass (grey arrow, Fig. 3.3) suggests an unobserved effect of time since fire. Although there is a slight negative correlation between time since fire and post-burn genet biomass (Fig. 3.4), the overall effect of time since fire via pre-burn genet biomass is still positive.

The changes in fireline intensity and heat per unit area associated with time since fire and total fuel did not influence post-burn genet biomass in the model. The effect of time since fire on

total fuel load was not significant, but total fuel did have a significant positive effect on both heat per unit area and fireline intensity (Fig. 3.3). However, the greater heat per unit area and fireline intensity with increased total fuel does not influence the resprouting response, as the direct effects of both heat per unit area (-0.04) and fireline intensity (0.02) on post-burn genet biomass were not significant in the model.

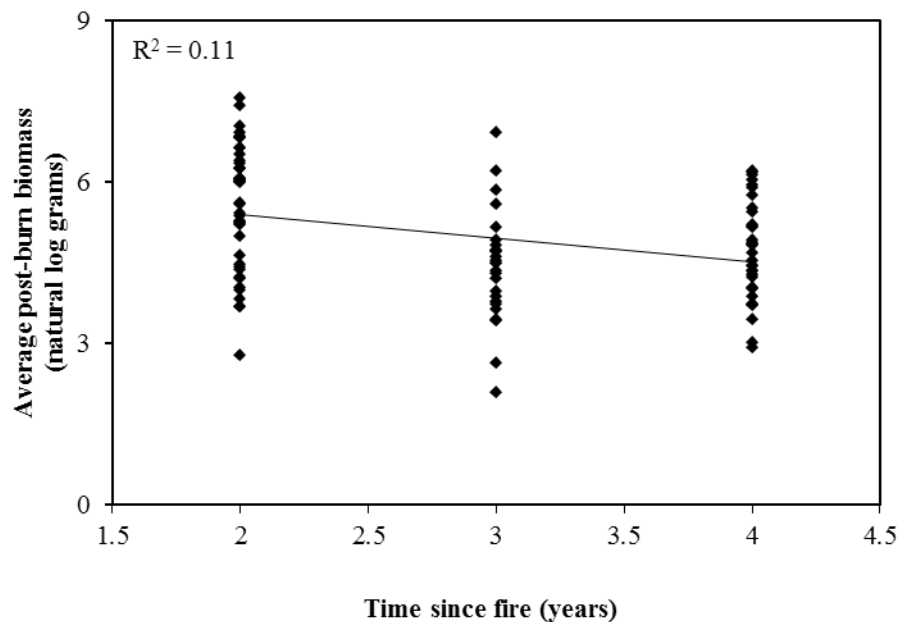


Figure 3.4. Scatterplot describing the relationship between time since fire and post-burn genet biomass. Points represent all genets included in analysis (both *Q. falcata* and *C. alba*).

Although fuel accumulates with longer time since fire intervals, this pathway was not significant in the model. This non-significant effect may be due to the variability of fuel loads among these plots, which have a great deal of overlap even though there is a slight increase in total fuel with time since fire (Fig. 3.5). The relatively low R^2 value for total fuel (0.21) also suggests that the model does not explain a high amount of the variance for total fuel load.

However, the year to year variation (shown as pathways from 2011) may be explaining a greater proportion of the fuel variability than time since fire alone.

The effects of 2011 related to time since fire and fuel are likely attributable to the timing of plot burns. The high correlation between 2011 and time since fire is the result of all 3yr and 4yr plots being burned in 2011. Similarly, the significant positive effect on total fuel (0.62) may be related to the greater fuel loads of 3-yr and 4-yr time since fire plots.

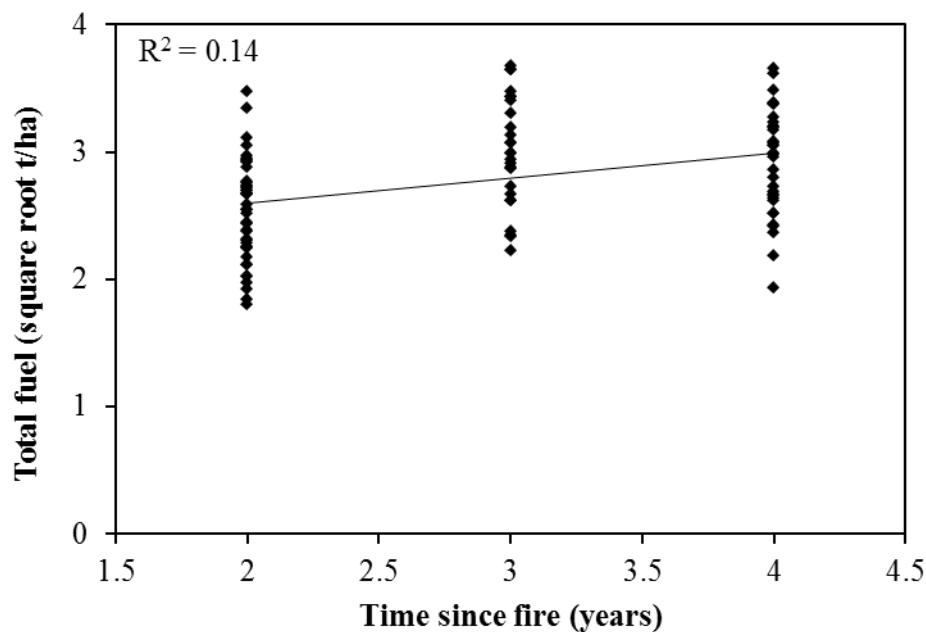


Figure 3.5. Scatterplot describing the relationship between times since fire and total fuel load.

The model suggested that growing season burns had a negative effect on post-burn genet biomass (-0.30). Growing season fires had a significant negative effect on fireline intensity (-0.18). However, the indirect effect on post-burn biomass via fireline intensity has virtually no effect ($-0.18 \times 0.02 = -0.004$). These paths suggest that, although fireline intensity decreases in

the early growing season, there are greater negative effects associated with topkill occurring at this time of year.

Ignition technique had significant effects on fireline intensity and heat per unit area. Head fires had greater fireline intensity (0.68), but reduced heat per unit area (-0.16), compared to backing fires. Nevertheless, the effects of head fire ignition technique did not result in an indirect effect on post-burn biomass mediated by the fire characteristics.

The effects of 2011 on fire characteristics and genet biomass may be related to drought conditions occurring in this year of the study. The direct effects of 2011 were positive for fireline intensity (0.19), and negative for heat released per unit area (-0.17), pre-burn biomass (-0.73), and post-burn biomass (-0.38). The direct effects of 2011 on fireline intensity and heat per unit area are misleading, and should be evaluated in terms of the total effect (i.e., sum of direct and indirect paths). The total effect of 2011 on heat per unit area was positive (0.26) when evaluated as both the direct effect and indirect effect via total fuel $[-0.17 + (0.62 \times 0.70) = 0.26]$. The total effect of 2011 on fireline intensity (0.28) was also positive $[0.19 + (0.62 \times 0.15)]$. These total effect suggest that both fireline intensity and heat per unit area increase under dry conditions. Although the paths through the fire characteristics did not influence post-burn genet biomass, the negative effects on pre-burn (-0.73) and post-burn genet biomass (-0.38) suggested that low precipitation in 2011 reduced the growth of resprouting stems.

The coefficients for paths from species to pre-burn biomass and post-burn biomass are interpreted as the effect of *C. alba* relative to *Q. falcata*. The negative coefficient for the effect on pre-burn biomass (-0.41) is attributable to the pre-burn biomass of *C. alba* (841.5 ± 162.1) being less than *Q. falcata* (1798.2 ± 161.9). The direct effect of species on post-burn biomass (0.15) was positive, suggesting that the growth rate of *C. alba* resprouts is greater. However, the

indirect effect of species on post-burn biomass via pre-burn genet biomass was negative ($-0.41 \times 0.86 = -0.35$), and the total effect is negative ($0.15 + -0.35 = -0.20$). This overall negative effect suggested that *C. alba* plants were generally smaller than *Q. falcata* at the time plots were burned and one year after prescribed fire treatments.

Discussion

Evaluation of the path analysis model shows greater support for the first hypothesis, that the effects of prescribed fire treatments on post-burn genet biomass are mediated via resource availability. There was no support for the hypothesis that fire characteristics would be a mediating factor in the response of post-burn genet biomass to prescribed fires. Additionally, the model reveals potential relationships associated with low precipitation that may impact resprouting response of hardwoods.

The positive effect of time since fire and negative effect of growing season fires on genet growth rates following topkill are attributable to temporal patterns on resource allocation. Without topkilling disturbances, hardwood genets can invest energy into both aboveground and belowground structures. When these larger individuals are topkilled, the greater pool of available root reserves enables faster growth of resprouts (Malanson and Trabaud 1988, Canadell et al. 1991, Dacy and Fullbright 2009). The negative effect of growing season reflects the reduced root reserves at the time genets are topkilled. These results provide additional support for the idea that growing season fires are more effective at reducing hardwood size and biomass (Robbins and Myers 1992, Glitzenstein et al. 1995, Drewa et al. 2006).

The results of the model do not support the hypothesis that differences in fire characteristics associated with prescribed fire treatments will influence hardwood resprouting. The influence of ignition pattern on fire characteristics was as expected, but there was no

subsequent effect of fireline intensity or heat per unit area on the resprouting response of genets. The lack of effect of fireline intensity and heat per unit area may be attributable to the fact that prescribed fires were conducted at a site that has experienced frequent fire for decades and therefore has relatively low fuel loads. Nevertheless, low intensity fires during the growing season (Chapter 2) resulted in topkill of genets, and led to a reduction in post-burn genet biomass.

The model revealed the potential effects of drought conditions and an unresolved negative correlation between time since fire and post-burn genet biomass. Prescribed fires in 2011 occurred in a year with below average precipitation, suggesting that the negative effects on pre-burn genet biomass and post-burn genet biomass may be related to drought conditions. Drought can reduce growth and aboveground biomass of hardwood genets, as there may be a greater investment in roots under drought conditions (Chiatante et al. 2005). The negative correlation between time since fire and post-burn genet biomass was surpassed by the positive effects of time since fire via pre-burn genet biomass. Nevertheless, this negative correlation suggests there are factors that are not accounted for in this model. For example, there may be greater competition for resources among resprouting grasses (Clarke and Knox 2009) and woody plants that have accumulated greater root biomass given a longer fire free interval.

The strong effects of drought conditions in 2011 demonstrate how climate can influence fuel conditions, fire characteristics, and hardwood resprouting. The impact of climate may become of greater importance in the future given the predicted changes associated with climate change and increased levels of atmospheric CO₂. It is predicted that the southeastern U.S. will experience increased temperatures, longer periods between rainfall events, and reduced soil moisture (EPA 2013). While the reduction in soil moisture and increased drought conditions may

reduce the growth rate of hardwood genets and their resprouts, as demonstrated by the path model, greater CO₂ can increase hardwood growth. Increased CO₂ in the atmosphere may be increasing the growth rate of woody species, increasing the potential for genets to attain sizes that are not susceptible to topkill at a faster rate (Bond and Midgley 2000, 2012). These changes in climate, which influence ecosystem processes, may require fire practitioners to adjust their objectives and planning in order to maintain savanna ecosystems, such as increased fire frequency to offset faster growth rates of resprouting hardwoods.

Even though the fire characteristics in the model did not have a significant effect on post-burn genet biomass, the effects of the model are dependent upon fires resulting in topkill to reduce aboveground genet biomass. Although growing season fires result in a lower resprout growth rate when genets are topkilled, prescribed fires in the growing season may be patchy and not topkill all genets if fuel moisture and relative humidity are high (Slocum et al. 2003, Knapp et al. 2009). Similarly, the low fuel loads in the first year after a prescribed fire can cause annual burns to leave unburned patches on the landscape. Patchy burns can result in longer time since fire intervals for unburned areas, leading patches of larger shrubs. The lack of effect of ignition technique suggests that backing fires can be used in situations that require low fireline intensity and have a similar effect on resprouting as a head fire. When weighing the trade-offs between the season and frequency of prescribed fires, fire practitioners should attempt to apply prescribed fires with the maximum frequency possible, and burn under conditions that are likely to support complete burns to avoid unburned patches on the landscape.

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CHAPTER FOUR: SEASON AND METHOD OF TOPKILL INFLUENCE RESPROUTING AND ROOT BIOMASS OF *QUERCUS NIGRA* SAPLINGS

Introduction

Most woody species in savanna ecosystems resprout following disturbances that kill aboveground plant tissues. When aboveground structures are killed (i.e. topkill), new stems are commonly produced from dormant buds at or below the soil surface by mobilizing energy stored in roots (Bowen and Pate 1993, Canadell and López-Soria 1998, El Omari et al. 2003). Resprouting potential of woody plants may be related to the method by which plants are topkilled, including fire, grazing, and mechanical land management activities. In savannas, a common topkilling disturbance is frequent, and this frequent topkill can limit the size and number of woody plants on the landscape (Waldrop et al. 1992, Schutz et al. 2009, Werner and Prior 2013) reducing the competition for light with herbaceous species (Scheiter and Higgins 2007). Pine-dominated ecosystems in the southeastern U.S. are one example of a savanna-type ecosystem where fire maintains the open savanna structure by topkilling woody species.

Broadleaf woody species in southeastern U.S. pine-dominated ecosystems are capable of resprouting when topkilled. The ability to rapidly accumulate aboveground biomass following topkill by fire is necessary in ecosystems where topkill is frequent (Hoffman and Solbrig 2003). Historically, broadleaf woody species (hereafter hardwoods) in pine ecosystems were topkilled by frequent fires, occurring primarily in the spring and summer months (Platt 1999, Huffman 2006, Stambaugh et al. 2011), and are limited to the surface vegetation layer (Drewa et al. 2006, Hoffman et al. 2009, Schutz et al. 2009). Hardwoods gain dominance over pines and herbaceous species when fires are excluded from the ecosystem (Waldrop et al. 1992, Haywood et al. 2001), changing the structure and reducing biodiversity (Scholes and Archer 1997, Glitzenstein et al. 2012). On the modern landscape, prescribed fire and fire surrogates (e.g., mowing, roller

chopping) can be used to control the size and number of hardwood stems (Menges and Gordon 2010). Determining how growth rates of hardwood resprouts respond to seasonal timing and methods of topkill is important for understanding how land management activities can influence hardwood demography.

Timing of disturbances in relation to seasonal cycles of plant resource allocation can affect resprouting. During the transition from the dormant season to the growing season, hardwoods in southeastern pine ecosystems transfer energy stored in the roots to aboveground structures for growth of new shoots and leaves (Woods et al. 1959). Thus, if topkill occurs during the seasonal low in resources during the growing season, the size and number of resprouting stems may be reduced (Woods et al. 1959, Glitzenstein et al. 1995, Drewa et al. 2002, Werner and Prior 2013). Mortality of hardwoods may also be greater when topkill occurs during the growing season (Glitzenstein et al. 1995), which can further limit the number of hardwoods on the landscape.

The interval between fires, and recovery rates of hardwoods post-fire, can influence root storage. The resprouting potential of individual plants is at least partially related to the amount of belowground storage at the time of disturbance (Bowen and Pate 1993, Landhäusser and Loeffers 2002). Individual plants with larger root reserves typically have faster recovery of aboveground biomass (Schutz et al. 2009) or larger resprouts (Kabeya and Sakai 2005). After removal of aboveground biomass, some species can fully recovery root storage pre-disturbance levels in as little as two growing seasons (Bowen and Pate 1993, Schutz et al. 2009). The ability of woody plants to persist in ecosystems with frequent fire is dependent upon plants recovering biomass (Grady and Hoffmann 2012).

How plants are topkill may also influence resprouting response. Current land management practices to control the size and number of hardwoods include prescribed fire and surrogates for fire such as roller chopping (Menges and Gordon 2010). Fire, which heats aboveground tissues and the soil surface, may do greater damage to dormant buds at the base of the plant or roots increasing the potential for mortality of plants in small size classes (Hoffman and Solbrig 2003). Extended heating of tissues to lethal temperatures may reduce the number of resprouting stems and thus overall resprouting biomass (Moreno and Oechel 1991, Bowen and Pate 1993; Kabeya and Sakai 2005, Schutz et al. 2009). Clipping, although sometimes used to mimic fire, may be more representative of the damage that would be caused by browsing. Identifying if the method of topkill influences aboveground structures (e.g., number of stems and stem height) and biomass of genets can improve our ability to understand differences in resprouting strategies to different methods of topkill.

The objective of this study was to determine how the season and method of topkill influence growth of aboveground resprouts and roots of hardwood saplings. I tested the following three hypotheses. 1) Topkill occurring when root reserves are low during the early growing season will result in reduced rate of recovery (stem height, number of stems, aboveground biomass and root biomass one-year post-topkill) and will have greater mortality compared to other seasons of topkill. 2) Fire results in reduced resprout size (number of stems, stem height, biomass) and greater mortality of genets compared to mechanical topkill, because plant tissues and meristems at the base of the plant are exposed to lethal temperatures during fires. 3) Topkill should reduce or slow the growth of roots because of reduced photosynthesis and the effect will be greater when topkill occurs in the growing season when root reserves are at a seasonal minimum. I tested these hypotheses by conducting an experiment with even-aged

hardwood saplings kept in nursery pots. Topkill treatments were applied at three times throughout the year, and aboveground and belowground biomass were sampled one-year post-treatment to determine if saplings had different responses to method and season of topkill.

Methods

The study was conducted on Tall Timbers Research Station (TTRS) located north of Tallahassee, Florida (30° 35' N, 84° 20' W). This area of north Florida is characterized by average annual high and low temperatures of 26.3 C and 13.3C, respectively, and annual precipitation of 1556 mm (Southeast Regional Climate Center). In this region, leaf flush of deciduous hardwoods typically occurs by March 30 (K.M. Robertson personal communication), and the growing season is considered to be early March through mid-November (Robbins and Myers 1992, Masters et al. 2007).

I used *Quercus nigra* (water oak) for this experiment. I chose *Q. nigra* because it is abundant on TTRS, widespread throughout the southeastern U.S., and may be representative of the resprouting response of other southeastern hardwoods found in pine-dominated ecosystems that resprout from root crowns (del Tredici 2001, see Drewa et al. 2006). *Quercus nigra* seedlings were collected from TTRS in August and September of 2008. Plants were initially planted in “cone-tainers” and kept in a shadehouse located on TTRS. In November of 2008, surviving seedlings were transferred to 1.0 gal nursery pots filled with a mixture of 50% topsoil and 50% sandy clay (soil obtained from Roberts Sand Co. Inc.). In the spring of 2009 and 2011, between 6 - 7 g of fertilizer (Osmocote Brand 18-6-12) was added to each pot to maintain a low level steady supply of nutrients to the plants. Pots were watered and weeded as necessary throughout the experiment, and pine straw mulch was used to cover the soil surface of each pot to protect against moisture loss and weeds.

Season and topkill treatments were applied in 2010 (one full growing season after planting) and 2011 (two full growing seasons after planting). The three levels of the season treatment were January (late dormant season), April (early growing season), and July (mid growing season). Within each year and season, three levels of the topkill treatment (clip, burn, control [i.e., no topkill]) were applied to 7 - 13 replicate *Q. nigra* saplings for a total of 207 plants (Table 4.1). Before treatments were applied, all plants were measured for number of stems, height of each stem, and basal diameter of each stem. Basal diameters of the stems were used to calculate the aboveground biomass using an allometric equation for *Q. nigra* determined at Tall Timbers Research Station and a nearby property (Robertson and Ostertag 2009). In addition to the plants treated for each season within the two years (six dates), I destructively sampled 7-13 plants to provide a baseline for comparison of belowground biomass at the time of topkill to the one-year post-treatment biomass measurements.

Table 4.1. Number of replicate plants (total n=207) each year that treatments were applied (2010, 2011) within each treatment combination of season (dormant, early growing, mid growing) and method (burn, clip, no topkill) of topkill. The number of plants surviving at the 1 year post treatment sampling data is also shown for each treatment combination within a given year.

Season	Method of topkill	Treated in 2010		Treated in 2011	
		Number of plants	Alive 1 year post	Number of plants	Alive 1 year post
Dormant	Burn	13	9	13	2
	Clip	13	11	13	5
	No topkill	13	11	13	4
Early growing	Burn	13	9	11	1
	Clip	13	13	10	4
	No topkill	12	12	7	4
Mid growing	Burn	13	6	12	5
	Clip	10	5	9	6
	No topkill	12	6	7	3

Method of topkill treatment levels for a given season and year were applied on the same day. To apply the clipping treatment, I used hand pruners to clip all stems approximately 2 cm

above the soil surface. Stems were clipped above the soil surface because mechanical treatments typically do not cut stems flush with the ground. I conducted burn treatments within the nursery pots using *Pinus palustris* (longleaf pine) needles as fuel. Needles were collected from TTRS and oven dried (24 hours, 80 °C), then 10.0-11.0 g of needles (dry biomass) were weighed out, allowed to rehydrate by exposure to ambient air, and placed on the soil surface within the pot (approximately 231 cm²) to be burned. The 10-11 g of pine needles spread over this area translates to 4.32-4.76 t/ha, which overlaps with the range of total one-hour fuel loads observed in a nearby old-field southeastern pine forest in north Florida (3.5-4.5 t/ha at 1-2 years since last fire) (Robertson and Ostertag 2007) and pine fuels measured in open areas of a longleaf pine forest in Louisiana (4.16 t/ha, W. J. Platt personal communication). To burn genets within the nursery pots, the pine straw mulch was removed, foil placed around the pot edge to protect the plastic, and the pine fuel placed on the soil surface surrounding the stem. To record the maximum temperature and residence time of each burn, I placed thermocouple wires (K-type 0.125 mm diameter, one second response time, Omega Engineering Inc.) connected to data loggers (Hobo U12-014, Onset Computer Corporation) within the bed of pine fuel, next to the hardwood stem. It was then ignited and allowed to burn. Any unconsumed fuel was collected from the soil surface following experimental fires, returned to the lab, and weighed to estimate fuel consumption. Assuming a standard energy content for longleaf pine needle fuel (Reid and Robertson 2012), these data were used to calculate the heat released per unit area (Johnson and Miyanishi 1995) and reaction intensity (rate of energy release within a given area) (DeBano et al. 1998) for all genets topkilled by fire. Fires resulted in 100% topkill of genets.

One year after treatment application, surviving plants were destructively sampled. For surviving genets, resprouting stems were measured (number, height, basal diameter), and genets

were separated into stems, leaves and roots. Aboveground tissue and roots were dried in a forced convection drying oven (80 °C) until they reached a constant mass (approx. 96 hours) at which time they were weighed.

Analysis

I performed analyses for genets treated in 2010 and 2011 separately. Twice as many plants died in the 2011 treatments (73% survival for genets treated in 2010 and 35% survival for genets treated in 2011), which could influence the interpretation or validity of the results. All statistical analyses were performed using SAS Software V9.3 (SAS Institute, Cary, NC). To test the first and second hypotheses, that season and method of topkill affect the growth rate of resprouts (measured as one-year post-treatment biomass), I used an analysis of covariance (ANCOVA). Season of treatment and method of topkill were independent variables serving as two main treatments, and analyses were conducted separately for each of the five response variables: average stem height, average number of stems, aboveground biomass, belowground biomass, and total biomass (all measured at one-year post-treatment). Biomass at the time of topkill was included in the model as a covariable, as it might have a relationship to root biomass and storage capacity and therefore capacity to resprout (Malanson and Trabaud 1988, Kabeya and Sakai 2005, Dacy and Fullbright 2009, Schutz et al. 2009). Models were determined for each response variable using PROC GLM SELECT, which aided in the selection of models that would meet the following criteria: 1) the covariate (aboveground biomass of genet at time of treatment) was retained within the final model, and 2) that the hierarchy of the model was maintained when interactions were significant. I used the backward selection method, where potential independent variables were: biomass at time of topkill, season, method of topkill, and all possible interactions. The level of significance for variables to remain in the model was $\alpha =$

0.05. I used the resulting models for each response variable (Table 4.2) to perform the ANCOVA analysis in PROC MIXED. I performed natural log transformations on all biomass variables to meet the assumption of normality of the ANCOVA. I used the Kenward-Roger method for calculating the denominator degrees of freedom to account for the differences in the number of replicate genets among treatment combinations, and Tukey-Kramer least-square means tests to perform pairwise comparisons of treatment effects.

The effects of topkill within each level of season treatment were analyzed using orthogonal contrasts. No-topkill genets were included with burned and clipped plants in the ANCOVA analysis, although we would not expect there to be an effect of season of treatment on genets which were not topkilled. Orthogonal contrast statements were constructed to compare topkilled genets (burn and clip) to the no topkill genets within each level of season (dormant, early growing, mid growing) for the aboveground biomass, belowground biomass, and total biomass of genets one-year post-treatment.

Interactions between main treatment effects and the covariable suggest that patterns are not consistent across treatments for all levels of the covariate. The interaction between the covariate (pre-burn biomass) and season or method of topkill treatment, observed for belowground biomass and total biomass of genets treated in 2011, was evaluated following the methods outlined by Littell et al. (2006). The steps were as follows: 1) compare slopes to evaluate if levels of treatment can be combined, 2) compare treatment levels at three values of the covariate, and 3) construct confidence bands at these three points. I evaluated each dependent variable at the levels of season or method treatment for three values within the range of the covariate (5 g, 20 g, 35 g) for comparison.

Table 4.2. Models selected using PROC GLM SELECT for each dependent variable (aboveground biomass, belowground biomass, total biomass, stem height, number of stems) for further analysis as ANCOVA models. The covariable (COV), aboveground biomass at time of treatment is included in each model, while inclusion of the method of topkill (METHOD) and season of topkill (SEASON) was dependent upon those treatments being significant in the model evaluation.

Dependent variable (one-year post-treatment)	Genets treated in 2010	Genets treated in 2011
Aboveground biomass	COV + METHOD + SEASON + METHOD*SEASON	COV
Belowground biomass	COV + METHOD	COV + METHOD + SEASON + COV*SEASON
Total biomass	COV + METHOD + SEASON	COV + METHOD + COV*METHOD
Stem height	COV + METHOD	COV + METHOD
Number of stems	COV + METHOD	COV

I ran a two-way ANOVA to determine if there were effects of season and year of on the observed fire characteristics.

I evaluated the probability of survival to one-year post-treatment based on season and method of topkill for each year separately. I used PROC GLIMMIX to evaluate a regression model with a binomial outcome (alive or dead) using the binomial distribution and logit link function options. I reduced the full model with season, method of topkill, estimated biomass at topkill, and all possible interactions to a model that only included season and method of topkill. The reduction was done because the biomass at time of treatment and interactions among treatments were not significant.

To test the third hypothesis, that season and method of topkill will influence root biomass recovery, I compared the root biomass of baseline measurements, topkilled plants, and non-topkilled plants at each sampling date (season and year combination). I used a mixed model analysis of variance, with the Kenward-Roger denominator degrees of freedom option due to the unequal number of replicates within treatment combinations (PROC MIXED). For each year, I tested for the effect of season (dormant, early growing, mid growing) and method of topkill (baseline, burn, clip, no topkill), and the interaction of season and method of topkill. These pairwise comparisons were performed using Tukey-Kramer least-square means tests.

Multiple pairwise tests were performed using this data set and the p-value was adjusted to reduce type I error. There were 12 independent tests, therefore the p-value for significance was reduced to 0.004 (0.05/12).

Results

Based on the GLM SELECT results, the ANCOVA models used to evaluate the dependent variables were different for genets treated in 2010 and 2011. For genets treated in

2010, method of topkill was included in models for aboveground biomass, belowground biomass, total biomass, stem height and number of stems (Table 4.2). Season was included in the models for aboveground biomass and total biomass, and the model for aboveground biomass also included the interaction of method and season of topkill (Table 4.2). For genets treated in 2011, method of topkill was included in belowground biomass, total biomass, and stem number models, and season included in the models for belowground biomass (Table 4.2). There were also interactions between the covariate and season and method of topkill for plants treated in 2011 (Table 4.2).

Recovery of biomass was reduced for genets treated in the growing season compared to the dormant season, although results were inconsistent for the two treatment years. For plants treated in 2010, I observed the aboveground biomass one year after treatment application to be 8.88 g lower in the early growing season compared to the dormant season and 11.29 g lower in the mid growing season compared to the dormant season (Fig. 4.1A). One-year post-treatment total biomass was also reduced for plants treated in the early and mid growing season of 2010 compared to the dormant season (Fig 4.1C). While the effect of season was significant for above and total biomass (Table 4.3), there was no difference in root biomass among seasons (Fig 4.1B), and season of treatment was not included in the ANCOVA analysis (Table 4.2). Belowground biomass one-year post treatment, for genets treated in 2011, was approximately 10 g greater in the early growing season compared to genets treated in the dormant and mid growing season (Fig 4.1B). The effect of season and method of topkill were not significant at the adjusted p-value of 0.004 for genets treated in 2011 (Table 4.3).

Burned and clipped plants typically had a greater number of stems and reduced stem height when compared to no topkill genets one-year post treatment. In the 2010 treatment year,

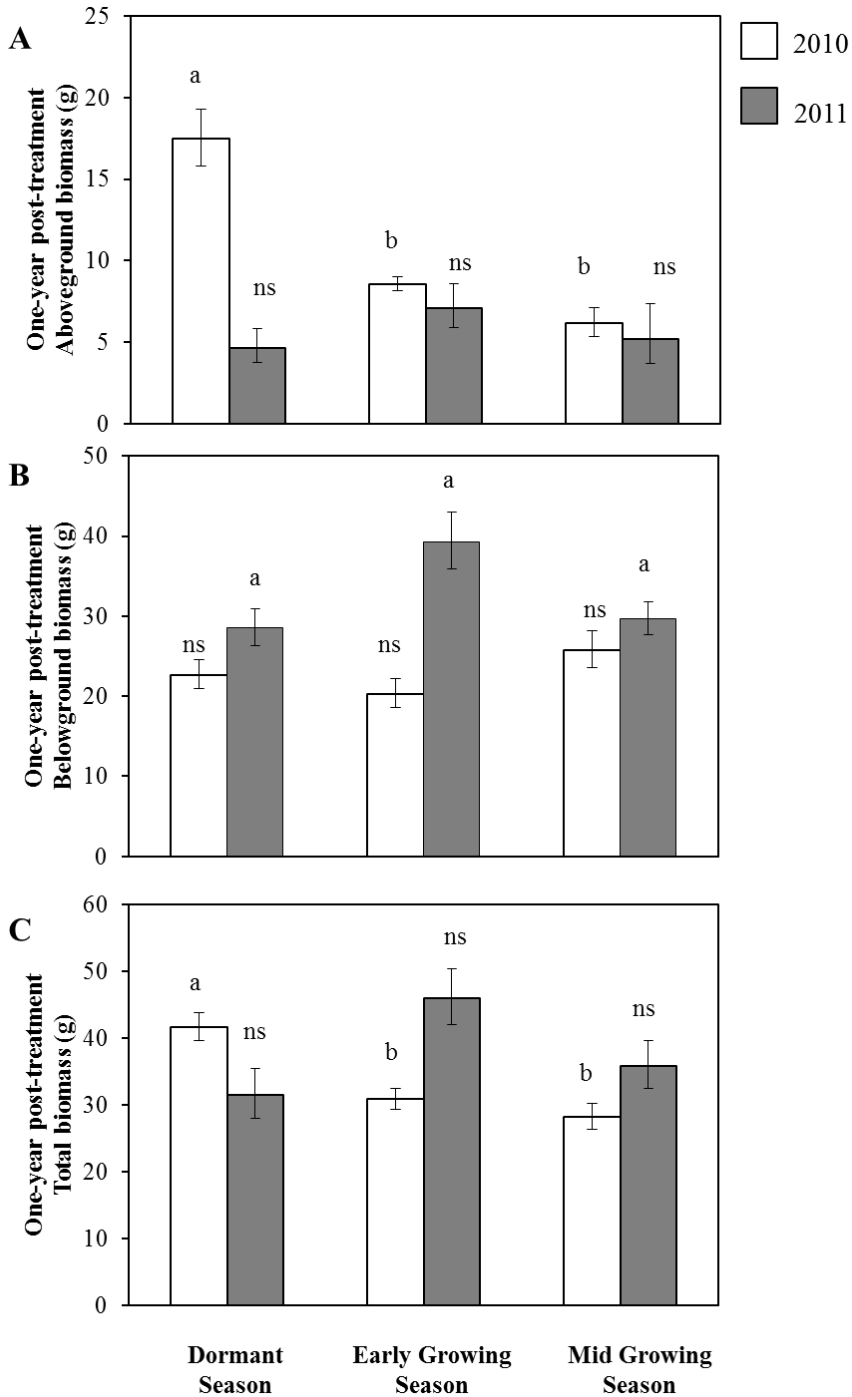


Figure 4.1. One-year post-treatment (A) aboveground biomass, (B) belowground biomass, and (C) total biomass, for each level of season of topkill (dormant, early growing, mid growing), for each treatment year (2010 and 2011). Values are back-transformed least-square means \pm 1 s.e. Different lowercase letters above bars indicate significant differences among seasons within a given year, when 'ns' appears above a bar this indicates treatment variables not included in the ANCOVA model.

Table 4.3. Effects of the covariate (COV), method of topkill (METHOD), and season of topkill (SEASON), and interactions when included in the ANCOVA model, on one-year post-treatment aboveground biomass, belowground biomass, and total biomass as indicated by *P* and *F* values (degrees of freedom in subscripts). Bold text indicates $p < 0.004$.

		Genets treated in 2010		Genets treated in 2011	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Aboveground biomass	COV	3.39 _{1, 71}	0.069	COV	0.75 _{1, 32} 0.3933
	METHOD	12.73 _{2, 71}	<0.0001		
	SEASON	23.09 _{2, 71}	<0.0001		
	METHOD * SEASON	4.53 _{4, 71}	0.0026		
Belowground biomass	COV	115.65 _{1, 77}	<0.0001	COV	9.83 _{1, 26} 0.004
	METHOD	20.20 _{2, 77}	<0.0001	METHOD	4.81 _{2, 26} 0.017
				SEASON	4.70 _{2, 26} 0.018
				COV * SEASON	5.33 _{2, 26} 0.011
Total Biomass	COV	73.67 _{1, 75}	<0.0001	COV	3.22 _{1, 28} 0.084
	METHOD	22.68 _{2, 75}	<0.0001	METHOD	6.00 _{23, 28} 0.007
	SEASON	14.25 _{2, 75}	<0.0001	COV * METHOD	4.56 _{2, 28} 0.019
Stem Number	COV	0.03 _{1, 78}	0.869	COV	1.17 _{1, 32} 0.289
	METHOD	43.99 _{2, 78}	<0.0001		
Stem Height	COV	12.74 _{1, 78}	0.0006	COV	2.81 _{1, 30} 0.104
	METHOD	40.02 _{2, 78}	<0.0001	METHOD	3.84 _{1, 30} 0.033

no-topkill genets typically had a single stem, burned plants had an average of 2 stems, and clipped an average of 3 stems (Fig 4.2A). In contrast, genets treated in 2011 had a similar number of stems for all topkill methods (Fig 4.2A). The resprouting stems of topkilled plants had less height than the no-topkill genets, but there was not a difference in height between clip and burn (Fig 4.2B). The effect of method of topkill on stem height and number was significant for genets treated in 2010 but not 2011 (Table 4.3).

Topkilled plants typically had reduced biomass compared to no-topkill plants, but method of topkill did not influence post-treatment biomass. One-year post-treatment aboveground biomass (Fig. 4.3A), belowground biomass (Fig. 4.3B), and total biomass (Fig. 4.3C) was less for topkilled plants (burn and clip) compared to no-topkill plants treated in 2010. The effect of method of topkill was significant (Table 4.3) but there was not a difference between burn and clip treatments. The aboveground biomass of plants treated in 2011 was not different among seasons and this treatment was not included in the ANCOVA model (Table 4.3). Belowground biomass and total biomass were typically less for plants topkilled in 2011 (Fig. 4.3B-C), but this was not a significant effect in the ANCOVA model (Table 4.3).

The orthogonal contrasts comparing topkill to no-topkill indicate that one-year post-treatment biomass of topkilled plants was different from no-topkill plants in 2010 but not 2011. There were significant differences ($p < 0.004$) between topkill and no-topkill for aboveground biomass in the early and mid growing season, belowground biomass in the mid growing season, and total biomass in the dormant and early growing season (Table 4.4). One-year post-treatment biomass of burned and clipped genets was equivalent to the no-topkill biomass in the dormant season of 2010 (Fig 4.4A), whereas the early growing season and mid growing season aboveground biomass of topkilled plants was approximately 5-7 g less than the no-topkill plants

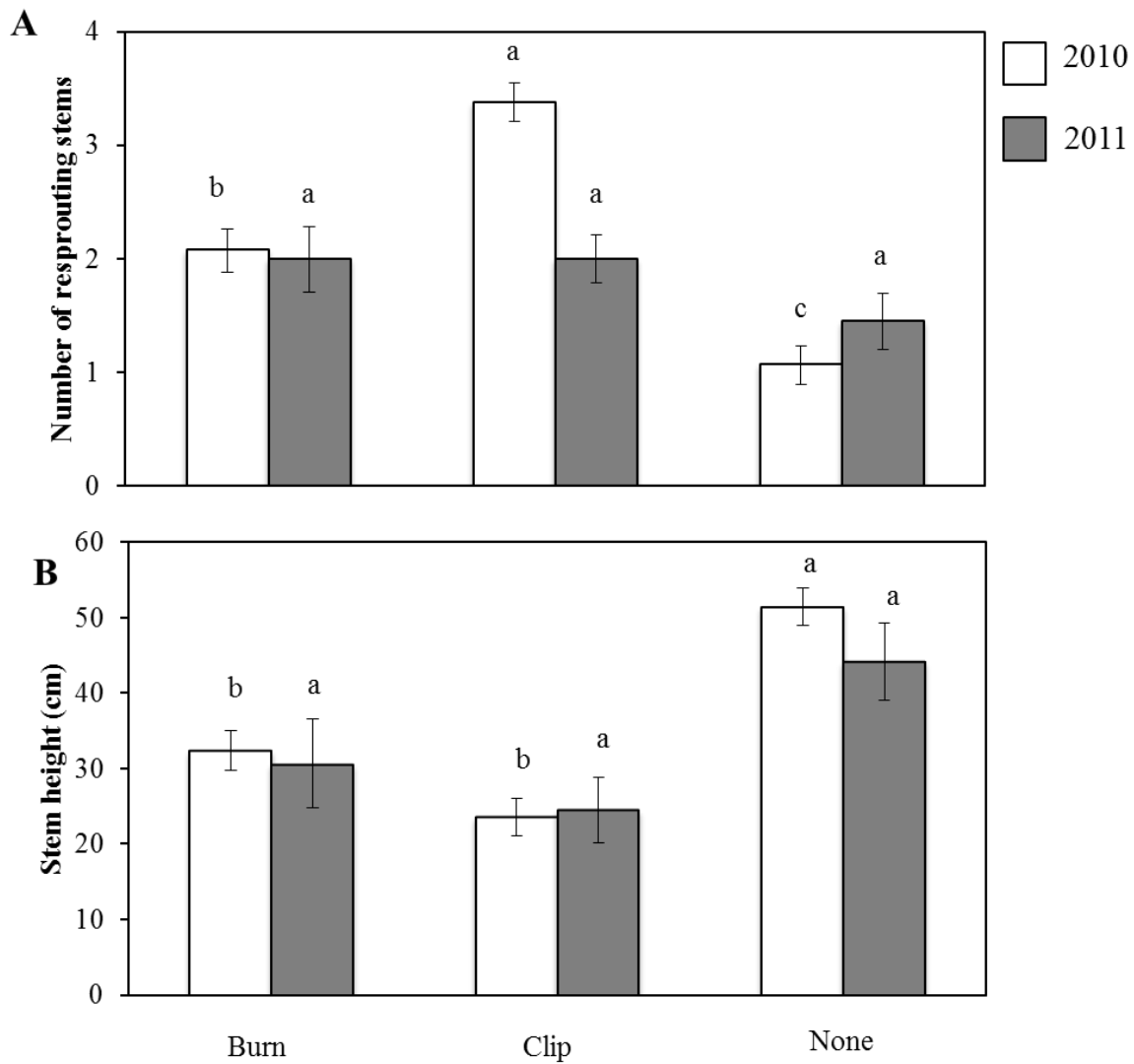


Fig 4.2. Number of stems (A) and average stem height (B) of genets one-year post-treatment, grouped by method of topkill (burn, clip, none), for genets treated in 2010 and 2011. Values are back-transformed least-square means \pm 1 s.e. Different lowercase letters above bars indicate significant differences among seasons within a given year.

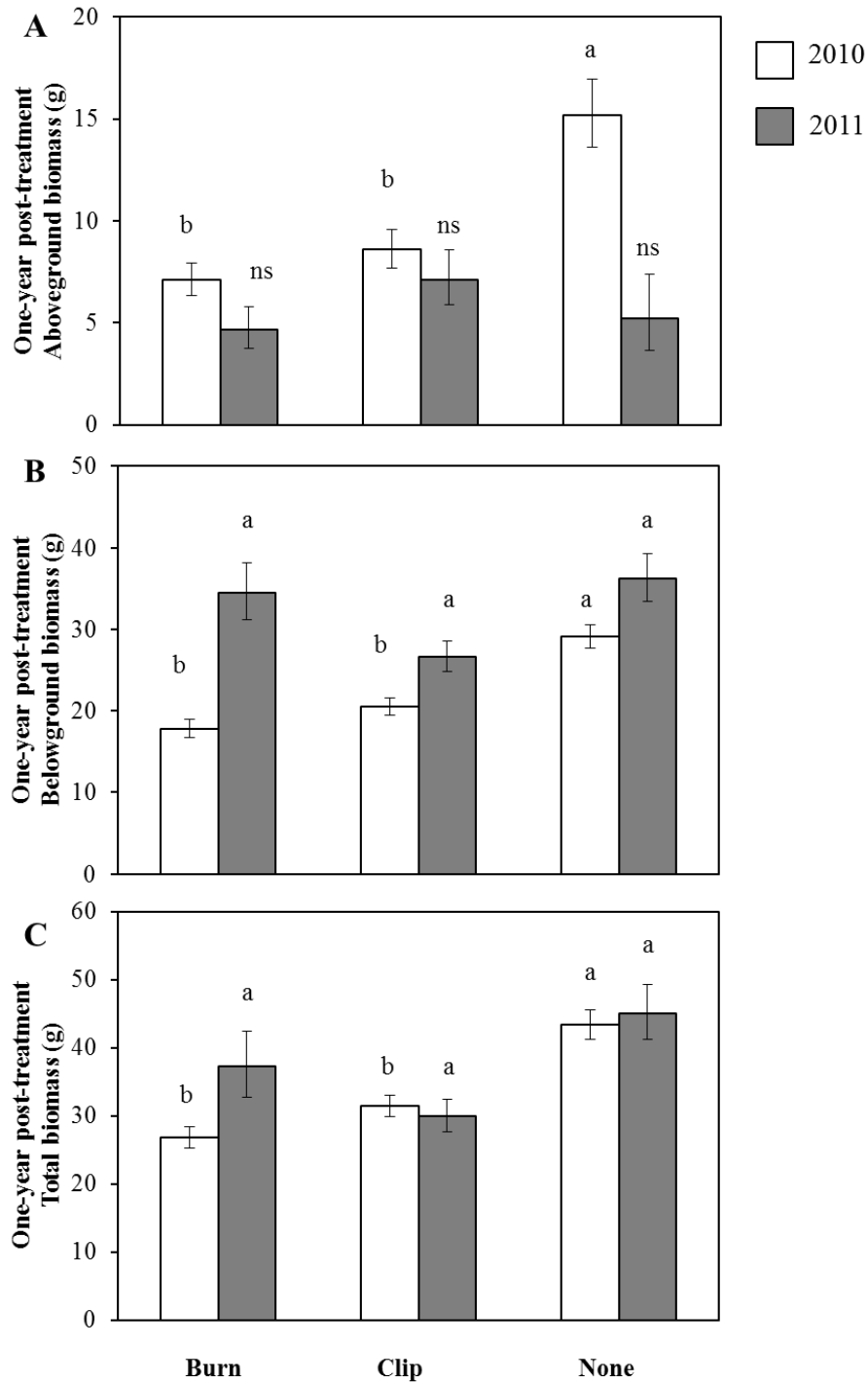


Figure 4.3. One-year post-treatment (A) aboveground biomass, (B) belowground biomass, and (C) total biomass, for each level of method of topkill (burn, clip, none), for each treatment year (2010 and 2011). Values are back-transformed least-square means \pm 1 s.e. Different lowercase letters above bars indicate significant differences among seasons within a given year, when ‘ns’ appears above a bar this indicates treatment variables not included in the ANCOVA model.

(Fig 4.4A). This pattern resulted in a significant interaction between method of topkill and season of topkill for the genets treated in 2010 (Table 4.3). Plants topkilled in 2011 did not show differences in one-year post-treatment biomass between topkilled and non-topkilled plants (Table 4.5) and there was not a similar pattern of one-year post-treatment biomass being equivalent for topkilled and no-topkill plants (Fig. 4.4B).

Table 4.4. Orthogonal contrasts of topkill treatments (burn and clip) compared to no-topkill treatments for aboveground biomass, belowground biomass, and total biomass in each season (dormant, early growing, mid growing). Bold text indicates $p < 0.004$.

	Genets treated in 2010		Genets treated in 2011	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Aboveground Biomass				
Dormant season	4.78 _{1, 71}	0.0320	1.83 _{1, 24}	0.1889
Early growing season	28.71 _{1, 71}	<0.0001	1.96 _{1, 24}	0.1744
Mid growing season	15.36 _{1, 71}	0.0002	2.52 _{1, 24}	0.1255
Belowground biomass				
Dormant season	0.01 _{1, 71}	0.9338	1.62 _{1, 24}	0.2159
Early growing season	7.58 _{1, 71}	0.0075	0.49 _{1, 24}	0.4895
Mid growing season	25.54 _{1, 71}	<0.0001	0.06 _{1, 24}	0.8118
Total Biomass				
Dormant season	10.76 _{1, 71}	0.0016	0.72 _{1, 24}	0.4039
Early growing season	22.54 _{1, 71}	<0.0001	1.13 _{1, 24}	0.2978
Mid growing season	4.22 _{1, 71}	0.0436	3.76 _{1, 24}	0.0642

Experimental fires varied slightly among seasons and years (Table 4.5). Fuel consumption and heat per unit area were less in the dormant season of 2011 than 2010. Temperatures were slightly greater in 2010 compared to 2011, but all were within the range of 400-1000 °C. Flaming and smoldering residence time was typically greater in the early growing season compared to the dormant and mid growing season, and residence times were greater in 2011 for all seasons. Results of the ANOVA are presented in Table 4.6.

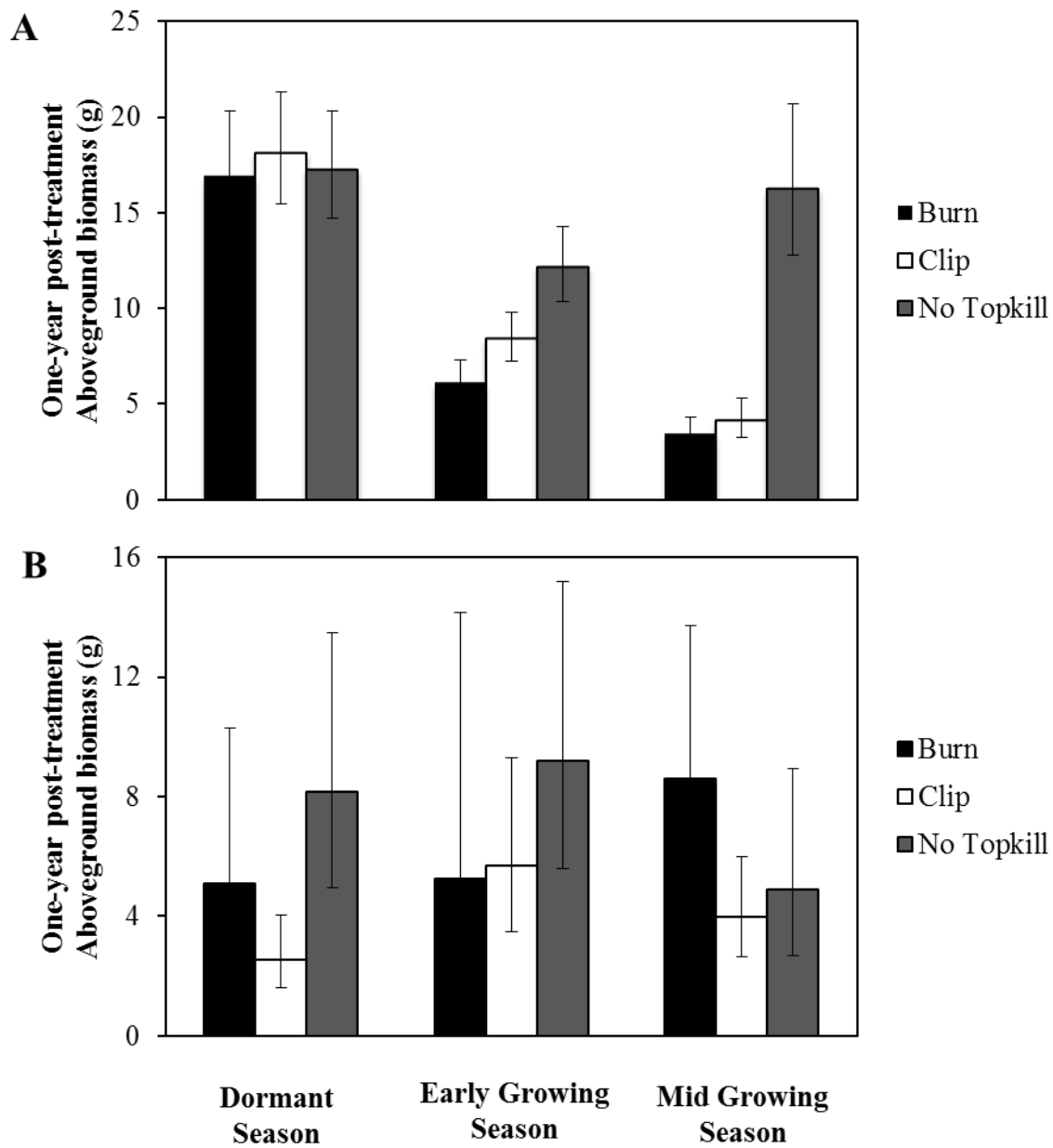


Figure 4.4. One-year post-treatment aboveground biomass for genets treated in (A) 2010 and (B) 2011 in response to method of topkill (burn, clip, none) and grouped by season of treatment (dormant, early growing, mid growing).

Table 4.5. Fire characteristics (maximum temperature, flaming and smoldering residence times, heat released per unit area, reaction intensity, and percent fuel consumed) observed for each season (dormant, early growing, mid growing) and year (2010, 2011) combination of burn treatments. Values are mean \pm 1 s.d.

	Treated in 2010			Treated in 2011		
	Dormant	Early growing	Mid growing	Dormant	Early growing	Mid growing
Maximum temperature ($^{\circ}\text{C}$)	788 \pm 225	878 \pm 153	792 \pm 217	707 \pm 279	505 \pm 259	531 \pm 295
Flaming residence time (sec)	48 \pm 17	65 \pm 16	49 \pm 22	42 \pm 27	94 \pm 40	69 \pm 40
Smoldering residence time (sec)	70 \pm 15	104 \pm 37	106 \pm 37	87 \pm 41	168 \pm 42	145 \pm 58
Heat per unit area (kJ/m^2)	88657 \pm 2664	81990 \pm 3871	82605 \pm 4648	77469 \pm 7607	83854 \pm 6679	83421 \pm 5705
Reaction intensity (kW/m^2)	2025 \pm 782	1305 \pm 458	3759 \pm 7176	2082 \pm 1187	2343 \pm 5297	1359 \pm 869
Percent fuel consumed	97.79 \pm 2.86	90.95 \pm 4.23	90.92 \pm 4.06	87.19 \pm 9.76	93.35 \pm 5.82	91.54 \pm 6.08

Table 4.6. Effects of season of treatment (dormant, early growing, mid growing), year of treatment (2010, 2011), and the interaction of season and year on fire characteristics (maximum temperature, flaming residence time, smoldering residence time, heat per unit area, reaction intensity, and percent fuel consumed) for genets topkilled by fire. *P* values are presented with associated *F* values (degrees of freedom are subscripts) and bold text indicates $p < 0.004$.

	Maximum temperature		Flaming residence time		Smoldering residence time		Heat per unit area		Reaction intensity		Percent fuel consumed	
	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>
Season	0.83 ₂	0.441	9.48 ₂	0.031	14.76 ₂	< 0.0001	0.004 ₂	0.996	0.25 ₂	0.775	0.31 ₂	0.734
Year	18.60 ₁	< 0.0001	4.84 ₁	0.0002	19.02 ₁	< 0.0001	5.19 ₁	0.026	0.23 ₁	0.630	3.54 ₁	0.064
Season * Year	2.41 ₂	0.098	2.54 ₂	0.084	2.24 ₂	0.1140	11.41 ₂	< 0.0001	1.32 ₂	0.275	9.26 ₂	0.003

For plants treated in 2011 the response to season and method of topkill depended upon how large the plants were initially, resulting in significant interactions of the covariate with treatments. I evaluated the interaction of the covariate with season and method of topkill that were significant in the ANCOVA model. The one-year post treatment total biomass for plants with a smaller pre-burn biomass (5 g pre-treatment biomass) was less for burned and clipped plants compared to no-topkill, but the one-year post treatment total biomass for larger plants (35 g pre-treatment biomass) was similar for all levels of topkill treatment (Fig. 4.5A). One-year post treatment belowground biomass was greatest for genets treated in the mid growing season at 5 g pre-treatment biomass, but at 35 g pre-treatment biomass of burned plants treated in the early growing season had the greatest belowground biomass (Fig 4.5B). These results suggest that treatment effects were not similar across the range of pre-burn biomass in 2011.

The probability of survival was influenced by season for plants treated in 2010, but there was no effect of season or method of topkill for plants treated in 2011. For genets treated in 2010, the probability of survival was approximately 4 times greater in the dormant season and 9 times greater in the early growing season compared to the mid growing season genets. The effect of season was significant (Table 4.7), but there was no effect of method of topkill. Only 35% of the genets treated in 2011 survived until the one-year post-treatment sampling dates, but there were no effects of season or treatment on survival (Table 4.7).

Table 4.7. Effects of season and method of topkill treatments on probability of survival for genets treated in 2010 and 2011. *P* values are presented with associated *F* values (degrees of freedom are subscripts) and bold text indicates $p < 0.004$.

		Genets treated in 2010	Genets Treated in 2011
Season	<i>P</i>	0.0010	0.122
	<i>F</i>	7.33 _{2, 107}	2.15 _{2, 109}
Method	<i>P</i>	0.130	0.072
	<i>F</i>	2.08 _{2, 107}	2.72 _{2, 90}

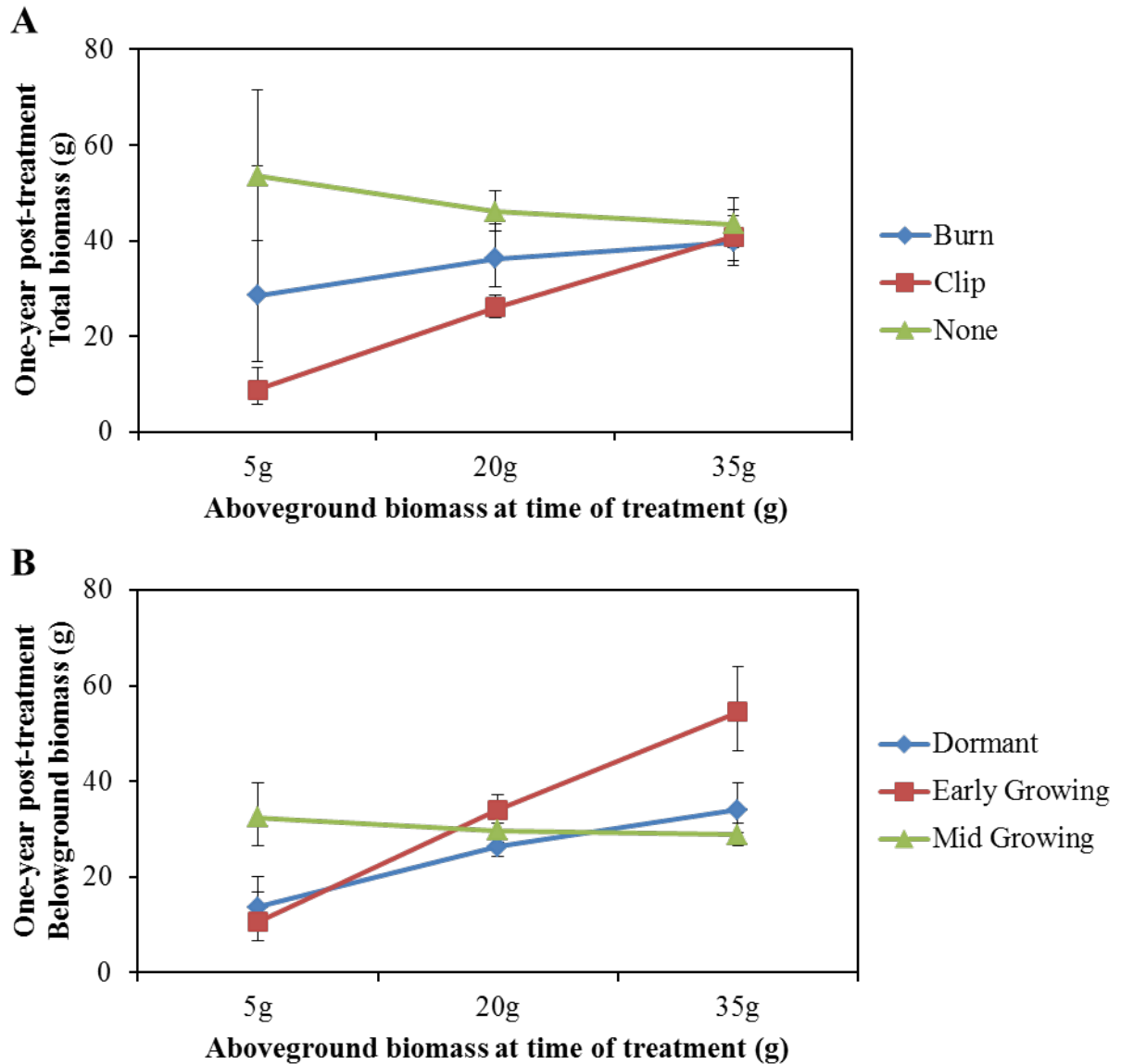


Figure 4.5. Evaluation of relationship between covariate (aboveground biomass at time of treatment) and dependent variables([A] one-year post-treatment total biomass, [B] one-year post-treatment belowground biomass) at three points within the range of the covariate (5g, 20g, 35g). Values are back-transformed means \pm 1 s.e. presented for (A) each level of method of topkill (burn, clip, none), and (B) each level of season of topkill treatment (dormant, early growing, and mid growing).

The observed patterns in root biomass, from the time of treatment to one-year post treatment sampling within each season of treatment, were different for genets treated in 2010 and 2011. The average root biomass of the baseline treatment in 2010 was 15 g. There was not a difference in belowground biomass between burned and clipped plants, but overall topkilled genets had a reduced root biomass compared to the no-topkill group, and a greater biomass than the baseline group (Fig. 4.6A). This difference among methods of topkill (baseline included as a treatment) for plants treated in 2010 was significant (Table 4.8). There was not an effect of season or method of topkill on root biomass of plants treated in 2011 (Table 4.8), and the mean root biomass show no consistent patterns (Fig. 4.6B).

Table 4.8. Effects of season and method of topkill, and their interaction, on one-year post treatment belowground biomass as indicated by *P* and *F* values (degrees of freedom included as subscripts with associated *F* value). Baseline biomass is included for each season within the two years treatments were applied. Significant values ($p < 0.004$) are indicated in bold text.

		Genets treated in 2010	Genets treated in 2011
Season		0.461	0.355
	<i>F</i>	0.88 _{2, 108}	1.06 _{2, 53}
Topkill		<0.0001	0.629
	<i>F</i>	8.22 _{3, 108}	0.58 _{3, 53}
Season*Topkill		0.928	0.811
	<i>F</i>	0.31 _{6, 108}	0.49 _{6, 53}

Discussion

The proposed hypotheses were generally supported by results from the 2010 treatments. In contrast, results from the 2011 treatments were less interpretable, probably as a result of the intervening effects of drought and heat stress during that year. In 2011 precipitation was 724.4 mm below average, and maximum temperatures during the months of the growing season were 1.05-3.67 °C above average in Tallahassee, Florida (Southeast Regional Climate Center). Although plants were watered frequently, the shadehouse offered little protection from these hot,

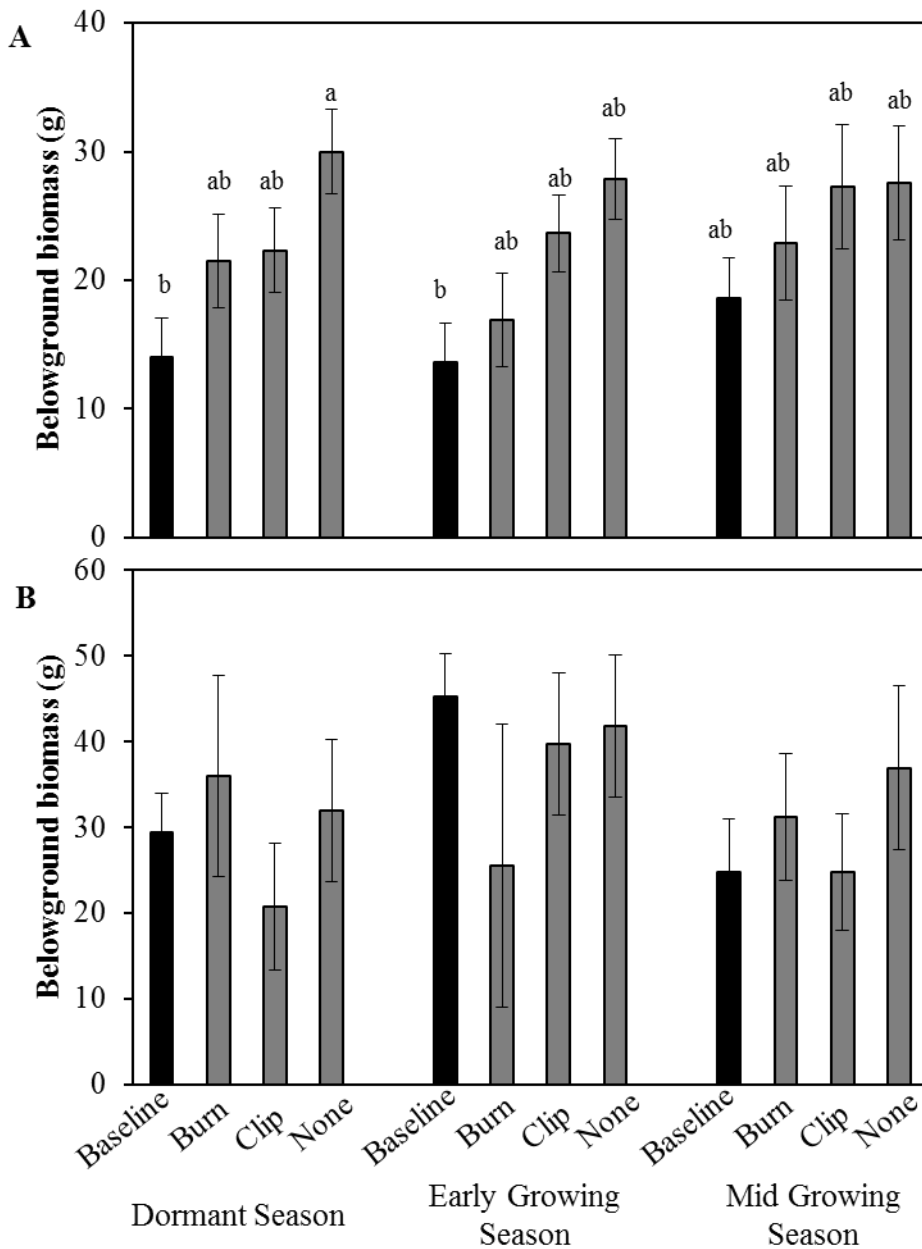


Figure 4.6. Belowground biomass of baseline genets destructively sampled at the time of treatment application (black bars) and genets sampled one-year post-treatment (grey bars) for genets treated in (A) 2010 and (B) 2011. Values are back-transformed least-square means \pm 1 s.e. for baseline and all levels of topkill (burn, clip, none) within each level of season (dormant, early growing, mid-growing). For genets treated in 2010 (A), different lowercase letters above bars indicate significant differences in means across all groups. Letters are not displayed for genets treated in 2011 (B) because there were no significant differences among groups.

dry, conditions. In this discussion I focus on the results of the 2010 treatment data unless otherwise specified, as the genets treated in 2011 had small sample sizes and uneven slopes in the ANCOVA models that could not be resolved.

My hypothesis that season of topkill would influence resprouting response was supported by the differences in one-year post-treatment aboveground biomass and total biomass, but not belowground biomass, number of stems, or stem height. The reduced aboveground biomass of resprouting stems topkilled in the early and mid growing season is attributable to topkill occurring when root reserves are at a seasonal low, which is consistent with other studies investigating the effect of season of topkill on resprouting of woody species (Waldrop et al. 1992, Glitzenstein et al. 1995, Drewa et al. 2006, Werner and Prior 2013). The differences in aboveground biomass but not belowground biomass one-year post topkill may be the result of hardwoods allocating greater resources to replenishing storage, rather than contributing to aboveground growth in the year after topkill occurs (Canadel and López-Soria 1998, Pelc et al. 2011). This allocation of resources to root storage rather than aboveground growth may be a trait selected for in ecosystems with frequent unpredictable disturbances (Iwasa and Kubo 2005). Recovery of resources in the interval between topkilling disturbances may allow for persistence of hardwoods in frequently burned ecosystems (Higgins et al. 2007, Schutz et al. 2009, Grady and Hoffman 2012).

The observation that burned genets have fewer resprouting stems than clipped genets supports my hypothesis that fire does greater damage to dormant buds. This result also suggests that an increase in hardwood stem density following disturbances may not represent an increase in biomass. Although these experimental fires were small, the characteristics were similar to fires in frequently burned southern pine communities. Although there was no difference in biomass

between burning and clipping, the greater number of stems of clipped plants may influence the surrounding microhabitat. A greater number of stems may increase shading of nearby herbaceous species, reduce flammability if there are a greater number of shed hardwood leaves, or buffer stems on the interior of the genet from contact with fine fuels and heating in later fires. However, this lack of apical dominance of genets after clipping may be a short term response with little lasting influence on the microhabitat.

While there were differences among fire characteristics associated with season and year of treatment application sample sizes were too small to detect any effects of fire characteristics on resprouting response. The maximum temperature, flaming and smoldering residence times, and reaction intensity were within the range observed for prescribed fires conducted on TTRS (1-2 years since previous fire; Chapter 2). Further, there is little evidence from the path model in Chapter 3 to suggest that differences in fire characteristics within the range observed in this study would influence resprouting response.

There was little support for the hypotheses that season or method of topkill would influence survival of genets. The increased mortality associated with topkill in the mid growing season of 2010 may be attributable to genets being less likely to survive topkill in the summer, or related to stress on the plants from being potted, as the number of surviving plants decreases over the course of the experiment. The high survival of genets topkilled in 2010 suggests that seedlings and saplings are unlikely to be eradicated by a single topkilling disturbance. Nevertheless, annual growing season fires can reduce the number of hardwood genets on the landscape as seen in long term studies of applied fire regimes (Waldrop et al. 1992, Herman 1995, Glitzenstein et al. 2012).

The limited root growth of topkilled plants supported my third hypothesis. The patterns observed for genets treated in 2010 were consistent, while there were no patterns for genets treated in 2011. The greatest gains in root biomass for genets treated in 2010 were for no-topkill genets, suggesting that topkill reduced root growth for clipped and burned plants (Chiatante et al. 2005, Chiatante et al. 2006). When fires are frequent, this reduction in root growth may limit the potential for individuals to resprout and achieve sizes that are less susceptible to topkill in subsequent fires (Schutz et al. 2009, Werner and Prior 2013). Nevertheless, topkilled plants had root biomass values equal to or greater than the baseline biomass, suggesting that root reserves are unlikely to show a net loss in root resources, even with annual topkill.

This study demonstrates that population dynamics of hardwood genets may be driven by survival and not resprout growth rate. Although the total biomass of genets was reduced for topkilled plants, there was not a reduction in root biomass below the average observed at the time topkill occurred. High survival and rapid recovery of root biomass suggests that frequent fires limit the opportunity for individuals to increase in aboveground size to the point of withstanding fires and growing into full sized trees (Grady and Hoffmann 2012, Werner and Prior 2013) but do not necessarily kill genets. Under these conditions, hardwoods established as a result of anthropogenic changes to the fire regime (Olson and Platt 1995, Drewa et al. 2002) are likely to persist when prescribed fires are applied. Nevertheless, frequent growing season fires reduce the potential for hardwoods to increase in size, and therefore can keep these ecosystems from becoming dominated by woody plants.

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CHAPTER FIVE: CONCLUSION

Summary

In this dissertation, I investigated the effects of time since fire, season, and ignition techniques of prescribed fires on fire characteristics and hardwood resprouting in a pine-dominated ecosystem in the southeastern United States. The time since fire, season of burn, and ignition technique of prescribed fires influenced fire characteristics, attributable to changes in fuel characteristics and weather with time and between seasons. These changes in fire characteristics, as well as application of fire versus mechanical topkill, did not have an effect on the one-year post-burn biomass of hardwood genets. Rather, the effects of time since fire and season of burn on one-year post-burn biomass were mediated by the size of the plant at the time of topkill and changes in resource allocation associated with season of burn. The results of these chapters demonstrate how the frequency and season timing of topkill are likely more important than the method of topkill or severity of fires for maintaining the open savanna-like structure of pine ecosystems in the southeastern United States.

Fire Characteristics

The response of fire characteristics to experimental treatments were primarily influenced by fuel characteristics. Greater fuel loads (3-yr and 4-yr time since fire plots) were associated with greater fireline intensity (rate of energy released per unit length of flaming front; kW/m) and heat released per unit area (kJ/m^2), and longer flaming and smolder residence times (duration of heating above 60 °C and 160 °C). At the same time, fuel bulk density increases as fuels become compacted over time, a response that would not be predicted by fire modeling software (Chapter 2). Fireline intensity and percent fuel consumption were the only fire characteristics influenced by season of burn and ignition technique, suggesting that fire characteristics

representing heating at the soil surface (including residence time, and heat per unit area) are unlikely to drive the observed differences in one-year post-burn biomass associated with season of burn or ignition technique in frequently burned southeastern pine-dominated ecosystems.

Hardwood resprouting in southeastern pine ecosystems

One-year post-burn biomass was influenced by the resources available to the genet at the time of topkill, but not the fireline intensity or heat per unit area (Chapter 3). There was also no difference in one-year post-treatment biomass between burned and clipped plants (Chapter 4). As the time since fire increases, hardwood genets can grow in size, and larger genets at the time of topkill produce larger resprouts (Chapter 3). The reduction in biomass associated with growing season fires (Chapter 3, Chapter 4) is consistent with observations of other studies (Waldrop et al. 1992, Glitzenstein et al. 1995, Drewa et al. 2006), and is attributable to the reduction in root reserves occurring early in the growing season when hardwoods put on new growth of shoots and leaves (Woods et al. 1959).

The shadehouse study provided insight into the response of roots to topkill, which is difficult to observe in the field. Topkilled saplings did not show a reduction in one-year post-treatment root biomass when compared to the baseline root biomass, suggesting that topkill does not result in a net loss of root biomass after one year (Chapter 4). Root growth was not as great for topkilled genets compared to no-topkill genets, but there was not a difference in one-year post-treatment root biomass between burn and clip treatments. The likelihood of mortality was the same for topkilled plants compared to genets which were not topkilled, demonstrating the capacity for resprouting of *Q. nigra*. The resprouting ability of *Q. nigra* under these experimental conditions may be representative of the response of similar hardwood species with root crown

resprouting in southeastern pine-dominated ecosystems, and can serve as a model for the expected changes in resprouting response and resource allocation.

Implications for conservation and management

Genets with adequate stored energy to resprout from fire are likely to persist on the landscape, and take advantage of fire free intervals to grow into larger size classes. My conceptual model in Chapter 3 included fire characteristics, which did not have a significant effect on one-year post-burn genet biomass. Based on the results of Chapter 3 and Chapter 4, I propose a model to explain the post-burn biomass of genets as a response to time since topkill and season of topkill being mediated by pre-burn biomass (aboveground and belowground) and seasonal changes in resource allocation (Fig. 5.1). Including an observed variable to quantify resource allocation in future studies would improve the understanding of mechanisms controlling

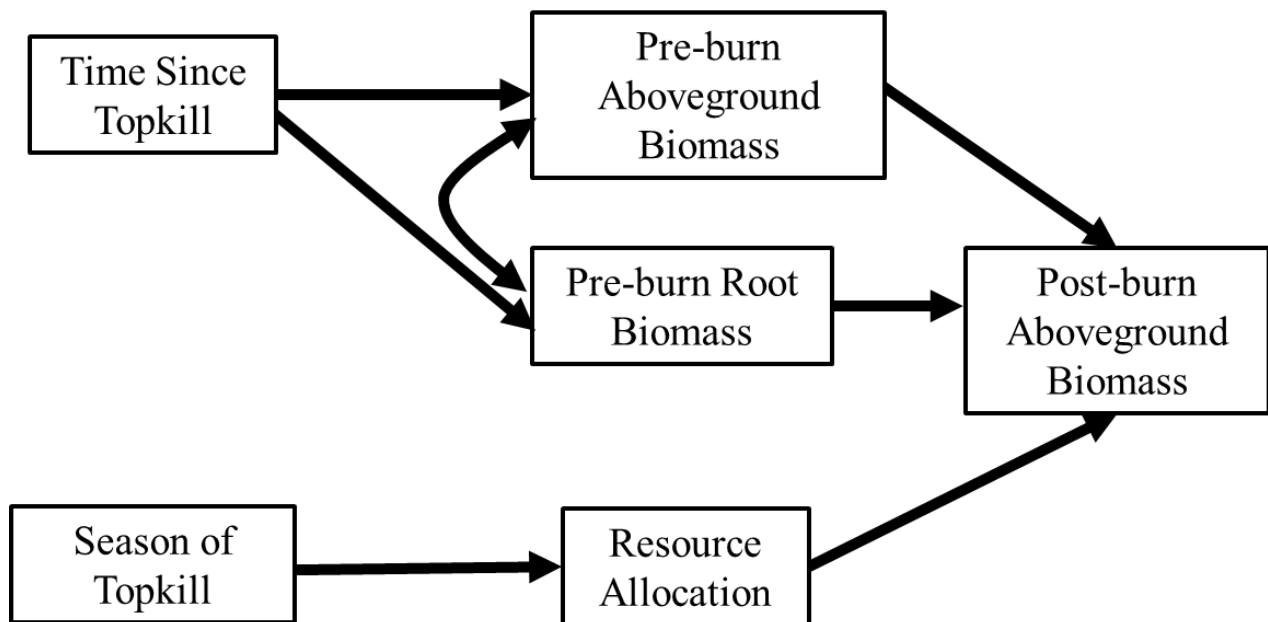


Figure 5.1. Conceptual model showing potential pathways mediating the effects of time since topkill and season of topkill on post-burn aboveground biomass.

hardwood resprouting response in frequently burned ecosystems and may give additional support to the hypothesis that resource allocation influences resprouting response.

Although the results of my dissertation are limited to the response of genets one-year post fire, it appears that frequency of fire may play a greater role in controlling hardwood biomass than season. As evaluated by the path model, time since fire has a stronger positive effect (i.e., greater one-year post-burn biomass) than the seasonality of fires (Chapter 3) for genets managed with frequent fire. High frequency dormant season fires may be more effective at controlling hardwood biomass when compared to growing season fires with a relatively longer fire return interval (e.g., annual dormant season burns compared to four year fire return interval growing season burns).

In both the field study and the shadehouse experiment I observed the influence of the drought conditions in 2011. I was able to interpret these effects in the context of prescribed fires and resprouting occurring under drought conditions for that year, although further study would be necessary to determine the specific effects of drought. Additionally the potential for CO₂ increase and climate change in the region may require fire practitioners to adjust their objectives and planning in order to maintain savanna ecosystems.

Management with prescribed fire must balance the ecological benefits of growing season fires with the potential for these burns to be patchy, due to the greater proportion of live fuel, greater live fuel moisture, and greater relative humidity. Growing season fires promote the flowering of wiregrass (Fill et al. 2012) and other herbaceous species (Platt et al .1988). However, prescribed fires planned for the growing season may also be delayed due to burn bans, or burn under conditions that leave unburned patches on the landscape. Hardwoods in unburned

patches, which then have an extended interval between fires, may attain sizes that will not be topkilled by future fires or will consistently resprout larger due an increase in root reserves.

The use of mechanical fire surrogates in place of, or in addition to, prescribed fires to ensure topkill needs further monitoring for long term effects. While there was no difference in one-year post-treatment biomass or mortality of *Q. nigra* between the two methods of topkill, the architecture of resprouting stems was different (Chapter 4). The reduced height may appear to open space and provide more light to the groundcover, but increased stem density associated with clipping may result in greater competition between woody and herbaceous species. Additionally, increased stem densities may create hardwood microhabitats that reduce the likelihood of stems to be topkilled by increasing hardwood leaf litter or buffering interior stems from fire.

Conservation of savanna ecosystems is dependent upon fire to suppress woody plants. Changes in land use that lead to an increase in woody plants are unlikely to be reversed quickly if fire is returned to the landscape, as the demographics of these species suggest that resprouting from stored root reserves can lead to persistence of woody species (Grady and Hoffmann 2012, Werner and Prior 2013). The results of this dissertation suggest that the frequency and seasonal timing of fire will have the greatest influence on resprout growth rates and dominance, and that frequent fires applied when root reserves are reduced are the most likely to reduce woody cover and maintain the open structure of savanna ecosystems.

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VITA

Tracy was born to Debra and Daniel Hmielowski and was raised in Massachusetts. Tracy attended Florida State University, in Tallahassee, Florida to pursue a degree in Biology. As an undergraduate, Tracy worked in the lab of Dr. Thomas Miller. Working with Dr. Miller provided an opportunity to gain field and laboratory experience. After graduating from Florida State in 2004, Tracy interned at Archbold Biological Station with Dr. Eric Menges in the Plant Ecology Laboratory, spent a summer as an intern in Yellowstone National Park, returned to Florida for an internship with United States Fish and Wildlife at Florida Panther National Wildlife Refuge, and spent a season working with The Nature Conservancy in central Florida. As an intern and seasonal employee, Tracy spent a great deal of time talking to people about ecology and the role of fire as a land management tool. It was these experiences that led to Tracy's desire to study the role of fire as a graduate student. Tracy began her doctoral degree at Louisiana State University in 2007 working with Dr. William Platt and Dr. Kevin Robertson at Tall Timbers Research Station. Currently, Tracy is a Ph.D. Candidate and will be graduating in August 2013.